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AUSTRALIAN INSTITUTE OF MARINE SCIENCE
MONOGRAPH SERIES

VOLUME 4

SCLERACTINIA OF EASTERN AUSTRALIA

PART III

Families Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectiniidae, Caryophylliidae, Dendrophylliidae

by

J. E. N. Veron

and

Michel Pichon

E. TURAK + L DEVANTIER

CORAL REEF ECOLOGY - CRC

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Dendrophylliidae

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Australian Institute of Marine Science
in association with
Australian National University Press
Canberra, Australia, London, England and
Norwalk, Conn., USA, 1979

First published in Australia 1980
Printed in Hong Kong for the Australian National University
Press, Canberra by Colorcraft Ltd

National Library of Australia
Cataloguing-in-Publication entry

Veron, J. E. N.
Scleractinia of eastern Australia. Part 3.

(Australian Institute of Marine Science. Monograph series; vol 4)
Bibliography
ISBN 0 7081 0768 0

1. Madreporaria. I. Pichon, Michel Maurice, joint author. II. Title. (Series)

593.6′0994

Library of Congress No. 78-304433

United Kingdom, Europe, Middle East, and Africa: Books Australia, 3 Henrietta St, London WC2E 8LU, England
North America: Books Australia, Norwalk, Conn., USA
Southeast Asia: Angus & Robertson (S.E.Asia) Pty Ltd, Singapore
Japan: United Publishers Services Ltd, Tokyo

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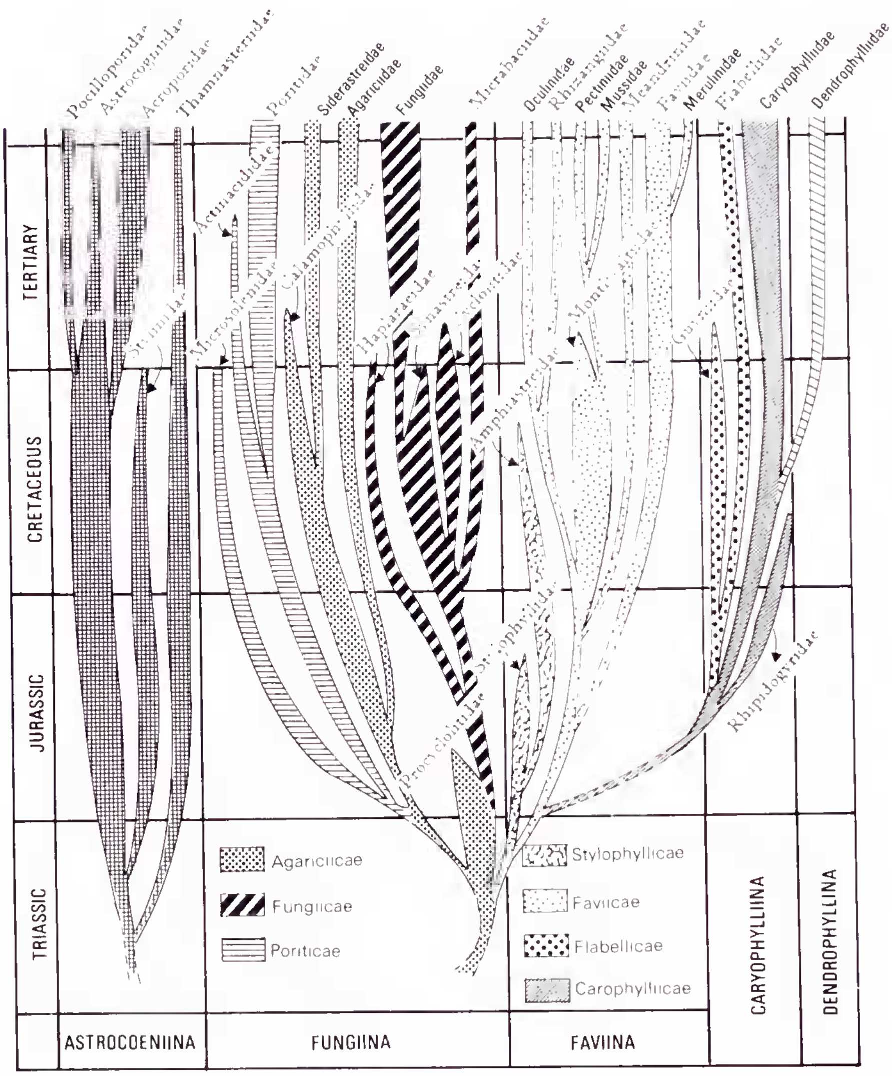

Pocilloporidae
Astrocoeniidae
Acroporidae
Thamnasteriidae
Poritidae
Siderastreidae
Agariciidae
Fungiidae
Micrabaciidae
Oculinidae
Rhizangiidae
Pectinidae
Mussidae
Meandrinidae
Faviidae
Merulinidae
Flabellidae
Caryophylliidae
Dendrophylliidae
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
Agariciicae
Fungiicae
Poriticae
Stylophyllicae
Faviicae
Flabellicae
Carophylliicae
CARYOPHYLLIINA
DENDROPHYLLIINA
ASTROCOENIINA
FUNGIINA
FAVIINA

I
Introduction

Scleractinia of eastern Australia Parts I-III includes descriptions of all known east Australian hermatypic species except those belonging to the two major families Poritidae and Acroporidae. Nine families comprising a total of 110 species are described in the present volume. Of these, 51 have not been previously recorded from eastern Australia, although only 5 have not been previously described.

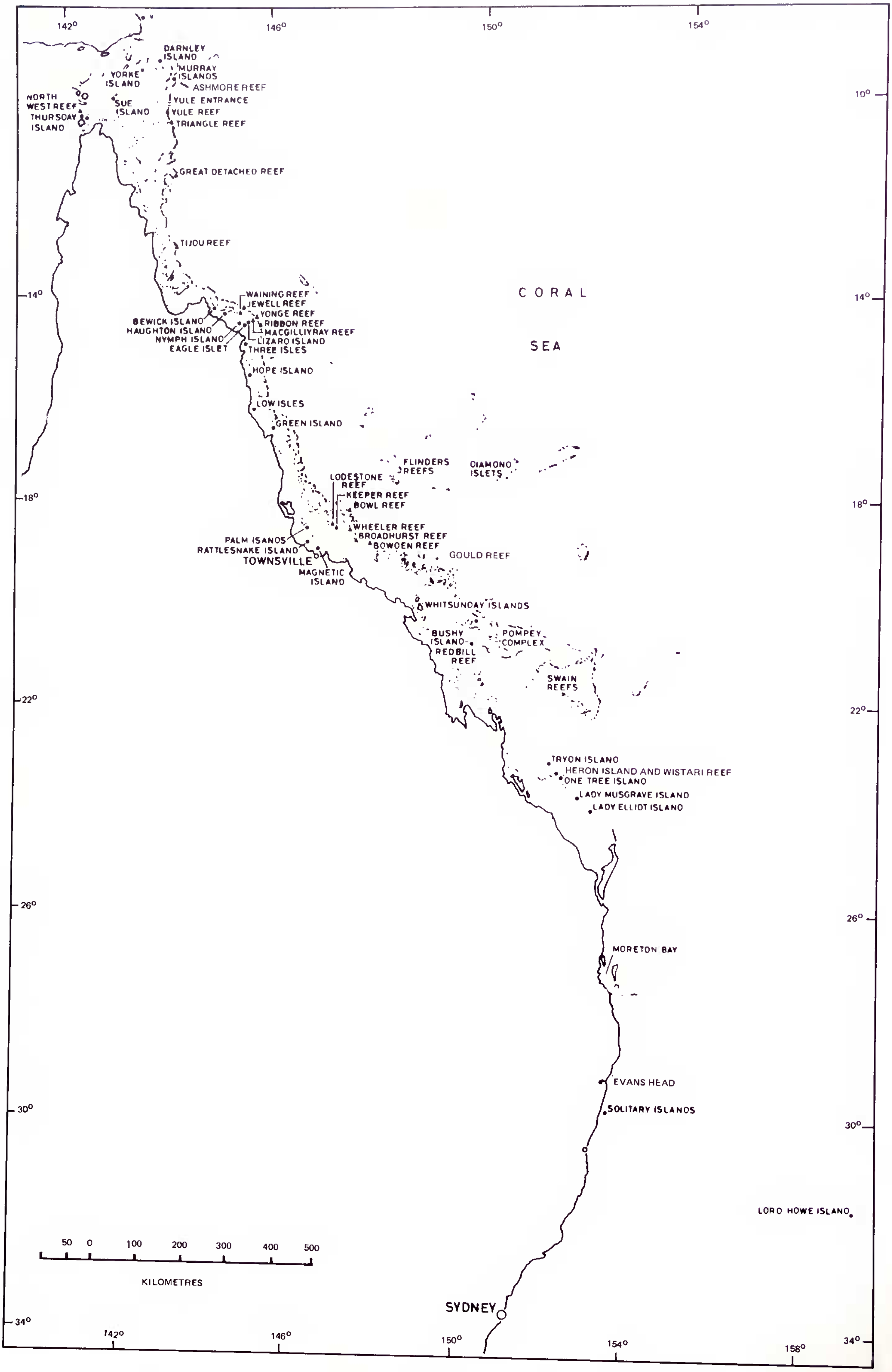
For many genera, phenotypic variation of species within the Great Barrier Reef can be precisely determined and used as a basis for detailed comparisons with collections and studies made elsewhere. Thus, the geographic range and full variability of these species can be determined and their synonymies and nomenclatural priorities established. For other genera, especially some which lack conservative skeletal characteristics or which have many closely related species, phenotypic variability within the Great Barrier Reef may be less easily defined. In such cases and especially with genera which have not received detailed study in the Indian Ocean, or species which have type localities far away from Indo-Pacific centres of diversity, synonymies may be tentative only, and nomenclatural priorities subject to change in the light of further study in these regions.

The corals described in this volume are from 4 of the 5 suborders of Scleractinia (Fig. 1). The very wide range of forms involved have necessitated widely differing taxonomic treatments. The taxonomy of some major genera e.g. *Fungia, Cycloseris* and *Symphyllia*, as well as many of the monospecific or minor genera, is relatively well established and has not required major change. Other genera, notably *Coscinaraea, Echinophyllia, Pectinia, Euphyllia* and (especially) *Turbinaria* are poorly known and major revisions have been necessary. These have required extensive *in situ* studies primarily to establish criteria for distinguishing co-occurring species, then to determine the full range of variation of these species.

Field methods used are essentially those described in Part I of this series. The present volume is based on the same collections as Parts I and II, supplemented by collections from detailed *in situ* studies made primarily at Lord Howe Island and Torres Strait (at opposite extremes of east Australian reef development) as well as at Heron Island, the Whitsunday Islands and Lizard Island in the Southern, Central and Northern Regions of the Great Barrier Reef respectively (Fig. 2).

Except where noted in the text, synonymies listed are based on extensive re-examination of all available type material affecting the validity of species names used, including all available junior synonyms considered valid in taxonomic publications of this century. Older type specimens which do not have taxonomic validity were studied only where questions of historical significance were involved.

Fig. 1 Evolutionary pattern of the Scleractinia after Wells (1956) indicating Indo-Pacific families containing hermatypic species. Those described in the present volume are indicated in bold print.



142°
146°
150°
154°
10°
14°
18°
22°
26°
30°
34°
158°
DARNLEY ISLAND
MURRAY ISLANDS
YORKE ISLAND
ASHMORE REEF
NORTH WEST REEF
SUE ISLAND
YULE ENTRANCE
YULE REEF
THURSDAY ISLAND
TRIANGLE REEF
GREAT DETACHED REEF
TIJOU REEF
WAINING REEF
JEWELL REEF
YONGE REEF
RIBBON REEF
MACGILLIVRAY REEF
LIZARD ISLAND
THREE ISLES
BEWICK ISLAND
HAUGHTON ISLAND
NYMPH ISLAND
EAGLE ISLET
CORAL
SEA
HOPE ISLAND
LOW ISLES
GREEN ISLAND
FLINDERS REEFS
DIAMOND ISLETS
LODESTONE REEF
KEEPER REEF
BOWL REEF
WHEELER REEF
BROADHURST REEF
BOWDEN REEF
GOULD REEF
PALM ISLANDS
RATTLESNAKE ISLAND
TOWNSVILLE
MAGNETIC ISLAND
WHITSUNDAY ISLANDS
BUSHY ISLAND
REDBILL REEF
POMPEY COMPLEX
SWAIN REEFS
TRYON ISLAND
HERON ISLAND AND WISTARI REEF
ONE TREE ISLAND
LADY MUSGRAVE ISLAND
LADY ELLIOT ISLAND
MORETON BAY
EVANS HEAD
SOLITARY ISLANDS
LORD HOWE ISLAND
50 0 100 200 300 400 500
KILOMETRES
SYDNEY

II
Principal Collecting Stations

Principal collecting stations used in the present study are those listed in Parts I and II of *Scleractinia of eastern Australia* together with those listed below. As previously noted, one or several biotopes are present at any one collecting station. Individual biotopes are not described.

All collections from stations below were made with SCUBA.

OUTER REEFS INCLUDING BARRIER REEFS

Biotopes of reef fronts

1-4. see Part I

61. see Part II

106. Ashmore Reef (Fig. 3); eastern slope of western reef, exposed to moderate wave action, steeply sloping, coral and rubble substrate; one collection, 10-20m.

107. Ashmore Reef (Fig. 3); western slope of western reef, exposed to moderate wave action, substrate of steep to vertical cemented reef rock with sand at 20m; one collection, 10-20m.

Biotopes of reef flats and very shallow lagoons

5, 6. see Part I

62, 63. see Part II

108. Submerged northern barrier reef (Fig. 3); reef flat (10m) and sides, exposed to strong currents and strong wave action, substrate of cemented reef rock; one collection, 10-30m.

Biotopes of reef backs

7-10. see Part I

64-66. see Part II

109. The barrier reef NE from Murray Islands, W side (Fig. 3); reef back, protected, steeply sloping reef rock and rubble substrate; one collection, 10-25m.

110. The barrier reef E from Murray Island (Fig. 3); reef backs, protected, gradually sloping, substrate of rubble and sand; one collection, 5-10m.

INNER REEFS AND ASSOCIATED CAYS AND LAGOONS

Biotopes of semi-enclosed lagoons

11, 12. see Part I

67-73. see Part II

111. Pandora Reef, N side; partly protected, partly enclosed, substrate of reef rock and rubble surrounded by sand; two collections, 2-15m.

Biotopes of reef outer slopes

13-22. see Part I

Fig. 2 Eastern Australian place names cited in the text.

74-81. see Part II

112. Redbill Island, W side; substrate of eroded reef sloping to sand, exposed to strong currents; one collection, 6-10m.

113. Gould Reef, W side; substrate of reef rock and rubble sloping to sand; one collection, 5-15m.

114. Gould Reef, E side; substrate of consolidated reef rock, sloping steeply to sand; one collection, 15-20m.

115. Heron Island reef, central S side; substrate of reef rock and consolidated rubble sloping steeply onto loose rubble, exposed to moderate currents; three collections, 5-15m.

116. Heron Island reef, central N side; substrate of consolidated rock deeply eroded into canyons with sand floors; two collections, 5-15m.

117. Wistari Reef, in channel adjacent to Heron Is.; substrate of reef rock, rubble and sand sloping steeply to sand, exposed to moderate currents; five collections, 5-20m.

118. Wistari Reef, N corner; substrate of consolidated rock and rubble sloping gradually to sand; two collections, 5-15m.

REEFS OF TORRES STRAIT (Fig. 3)

The Torres Strait region can be divided into four longitudinal zones each containing a distinctive complex of islands and reefs. The first (western) zone includes a series of E-W oriented reefs bounded in the south by high islands and mangrove cays. Tidal currents are strong and the water shallow and turbid. The second zone includes the large Warrior and Dungeness Reefs, with a N-S orientation. Tidal currents are strong in passes between reefs and the water turbid. The third zone includes a wide variety of islands and reefs increasing in density towards the east. Reef areas are separated by relatively deep, clear water. Coral growth is mostly luxuriant and species diversity is high. The fourth (eastern) zone is comprised of an outer barrier of deltaic and dissected reefs (Veron, 1978).

119. Jervis Reef, NE and E side; substrate of reef rock gradually sloping to rubble, exposed to strong currents; three collections, 2-12m.

120. Warrior Reef, SE corner; substrate of steeply sloping reef rock and rubble to muddy sand; one collection, 8-25m.

121. Warrior Reef, E side (9°40′S. lat.); substrate of deeply ended reef rock, sand and rubble sloping to sand; one collection, 5-12m.

122. Dungeness Reef, SE face; substrate of gently sloping rubble to sand; one collection, 10-25m.

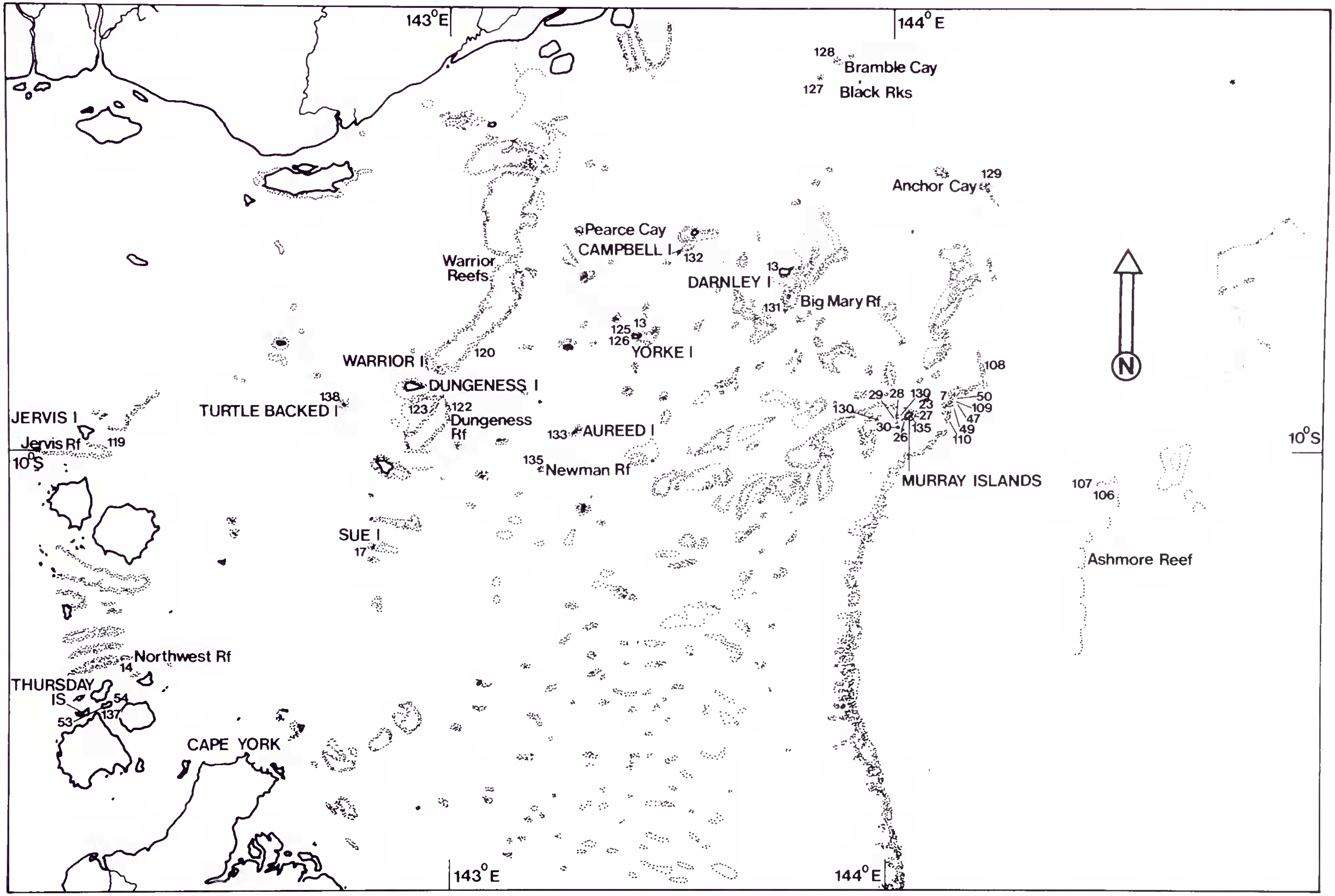
123. Dungeness Reef, NW face; substrate of steeply sloping rubble to sand; one collection, 10-15m.

124. Pearce Cay, S side; substrate of eroded reef rock and sand sloping gradually; one collection, 5-15m.

125. Yorke Island, NW corner; substrate of vertical reef rock to 10m thence steep rubble slope to 25m; two collections, 5-15m.

126. Yorke Island, N side; substrate of rubble and sand sloping gently; two collections, 7-20m.

Fig. 3 Torres Strait and surrounding islands and reefs. Principal collecting stations are numbered.


143°E
144°E
128
Bramble Cay
127
Black Rks
Anchor Cay
129
Pearce Cay
CAMPBELL I
132
Warrior
Reefs
13
DARNLEY I
131
Big Mary Rf
13
125
126
YORKE I
WARRIOR I
120
DUNGENESS I
138
TURTLE BACKED I
123
122
Dungeness
Rf
JERVIS I
Jervis Rf
119
10°S
133
AUREED I
135
Newman Rf
108
29
28
130
7
50
130
23
27
109
47
30
135
49
26
110
MURRAY ISLANDS
107
106
Ashmore Reef
10°S
N
SUE I
17
Northwest Rf
14
THURSDAY
IS
54
53
137
CAPE YORK
143°E
144°E

127. Black Rocks, E side; substrate of vertical rock to 12m thence sloping rock and sand; one collection, 8-12m.

128. Bramble Cay; substrate of steeply sloping rock, rubble and sand, exposed to seasonal low salinity; three collections, 5-20m.

129. Anchor Cay; substrate of steep, eroded reef rock to sand; two collections, 10-20m.

130. Reef W of Maer Island, NW edge; substrate of rubble and reef rock sloping to sand; two collections, 8-22m.

131. Big Mary Reef, SW edge; substrate of rubble and sand sloping to soft mud; two collections, 5-30m.

132. Campbell Island, SW edge; substrate of reef rock and rubble sloping to sand; one collection, 5-10m.

133. Aureed Island, NW and SE sides; substrate of gently sloping reef rock and sand; two collections, 10-30m.

134. Newman Reef, N edge; irregular substrate of rock and sand sloping to 30m; one collection, 15-20m.

HIGH ISLANDS (except Lord Howe Island)

Biotopes of sandy or partly sandy flat ocean floor

23-25. see Part I

Biotopes of the front of fringing reefs

26-38. see Part I

82-83. see Part II

135. Maer Island (Murray Island) S point (Fig. 3); substrate of reef rock and rubble sloping steeply to sand, exposed to moderate wave action; one collection, 5-15m.

Biotopes of intertidal and sub-intertidal mud flats

39, 40. see Part I

84-86. see Part II

Biotopes of the zone of coral growth on the protected side of high islands

41-43. see Part I

87-98. see Part II

136. Wai-Weer Island (Fig. 3); substrate of sand and rubble sloping to sand, turbid water with strong currents; one collection, 2-8m.

137. Thursday Island, SW edge (Fig. 3); steeply sloping substrate of sand and rubble, turbid water exposed to strong currents; one collection, 2-7m.

138. Turtle Backed Island, W side (Fig. 3); steeply sloping substrate of rubble to sand; one collection, 2-11m.

139. Between Maer and Dewar Islands (Murray Islands) (Fig. 3); irregular substrate of reef rock, rubble and sand; one collection, 10-25m.

140. Hazelwood Island (Whitsunday Islands), NW side; irregular substrate of reef rock, rubble and sand; one collection, 3-8m.

141. Hook Island, Whitsunday Islands, N side; promontory of rock sloping irregularly onto sand; turbid water; six collections, 2-15m.

Lagoons of high islands

99, 100. see Part II

Biotopes of muddy ocean floors

44-46. see Part I

101, 102. see Part II

Tidal channels between reefs exposed to currents

49-52. see Part I

103-105. see Part II

Remaining non-reefal biotopes

47, 48, 53-60. see Part I

LORD HOWE ISLAND

A detailed account of the diversity of coral communities of Lord Howe Island is given elsewhere (Veron & Done, 1979). For comparative purposes, coral communities are arbitrarily divided into (a) those of the lagoon (including reef 'passages' and 'holes'), (b) the reef and outer slope, and (c) the non-reefal eastern and northern bays and promontories.

Biotopes of the lagoon

142. The lagoon; substrate of flat sand, two collections, 0-2m.

143. Lagoon 'passages'; a wide variety of rubble and sand substrates sloping steeply onto sand; passages penetrate the lagoon reef; five collections, each at varying depths between 0-20m.

144. Lagoon 'holes'; substrate of flat sand forming depressions in the lagoon floor; four collections, 1-4m.

Biotopes of the lagoon reef

145. The reef front; substrate of eroded reef rock, rubble and sand sloping gradually to smooth, horizontal, reef rock and sand; two collections, 0-30m.

146. Reef flat holes; substrate of reef rock and rubble forming holes inside the reef front; two collections, 0-5m.

Biotopes of non-reefal bays and promontories

147. Northern and eastern bays and promontories; substrate of eroded volcanic rock sloping very irregularly to sand, exposed to strong wave action; five collections, 1-15m.

III
Family Agariciidae Gray, 1847

The extant Agariciidae are all hermatypic and colonial with colony formation mainly by intratentacular budding. Walls are synapticulothecal, poorly developed or absent. Septa are fine, regularly spaced and ornamented, and are mostly confluent between centres. Endothecal dissepiments are mostly absent.

Of the 6 extant genera of Agariciidae, all except *Agaricia* (restricted to the Atlantic Ocean) are widespread throughout the main Indo-Pacific coral reef regions, including the Great Barrier Reef. Of the Indo-Pacific genera, *Gardineroseris* and *Coeloseris* are monospecific and *Pachyseris* is a well defined genus containing 2 or 3 closely related species. The remaining 2 genera, *Leptoseris* and *Pavona*, include a very wide range of species, some of which have uncertain affinities.

Of all major east Australian coral genera, *Leptoseris* is perhaps the least well known, with only one species, *L. gardineri*, having been previously recorded from the Great Barrier Reef.

GENUS *PAVONA* LAMARCK, 1801

Generic synonymy

Pavona Lamarck, 1801.

Pavonia Lamarck, 1816.

Lophoseris Edwards & Haime, 1849c.

Type species *Madrepora cristata* Ellis & Solander, 1786.

Characters of the genus

Colonies are massive to foliaceous with mostly bifacial fronds. Corallites are mostly compact with walls poorly developed or absent.

Introduction

The taxonomy of *Pavona* is dominated by the large number of species of Lamarck and Dana and later of Verrill, Brüggemann and Gardiner. These early authors mostly studied collections from a very wide geographic range and, with the exception of Dana, usually recognised distinct species within their own collections but gave relatively little attention to synonymy with nominal species from other collections.

Subsequent studies of *Pavona* species, summarised in Fig. 4, have resulted in varying conclusions mostly based on small collections, indicating very limited variability, from restricted geographic areas. Clearly, this genus is in need of revision based upon detailed regional studies. Only then can the geographic range of species be determined and their variation within that range appreciated.

Eight species are recognised from Eastern Australia. These are all common and, despite the great variability within most species, all are readily distinguished. However, it is emphasised that these species clearly represent only a small proportion of Indo-Pacific *Pavona*.

The genus is generally divisible into leafy and non-leafy forms, the former group having the majority of true species (as well as nominal species). Only two of these, *P. cactus* and *P. decussata*, have been found in the Great Barrier Reef. Two other

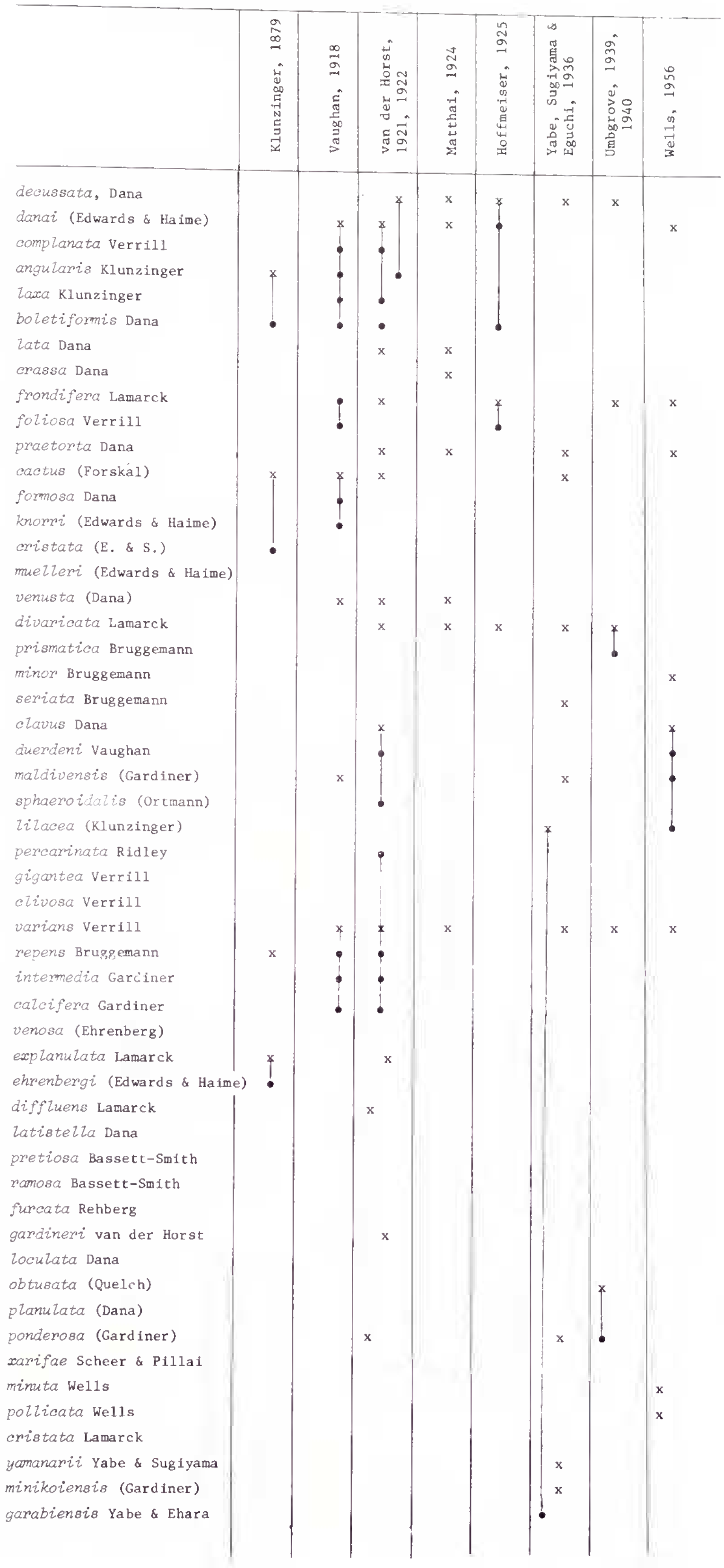


Fig. 4 The synonymy of nominal species of *Pavona* and species of other genera previously placed in *Pavona* according to the authors indicated. Species names considered valid by each author are indicated by a cross. Synonyms are indicated by a dot and joining line. Generic designations are not indicated.

widespread species, or species groups, generally known as *P. frondifera/danai/cristata* and *P. divaricata/prismatica* have not been found, and thus the present study does not add greatly to the understanding of the interrelationships of leafy *Pavona* species.

The non-leafy (massive or laminar) species are well represented in the present series. These have a very wide variety of form and structure, more so than is found in most scleractinian genera. However, subgroups within *Pavona* are not readily distinguished and no subgenera are retained in the present study. The remaining species have uncertain affinities, both among themselves and with species of other genera, notably *Leptoseris*.

Pavona cactus (Forskål, 1775)

Synonymy

Madrepora cactus Forskål, 1775

Pavona cactus (Forskål) Klunzinger (1879); Studer (1901); von Marenzeller (1907); Gravier (1911); Vaughan (1918); van der Horst (1921); Matthai (1923a, 1948c); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Crossland (1938); Ma (1959); Pichon (1964); Scheer (1967).

Pavona praetorta Dana, 1846; Verrill (1864); Quelch (1886); van der Horst (1921, 1922a); Matthai (1924); Hoffmeister (1925); Faustino (1927); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Wells (1954); Nemenzo (1955a); Ma (1959).

Pavona formosa Dana, 1846; Verrill (1864); Quelch (1886).

Pavona venusta Dana, 1846; Studer (1880); Verrill (1864); Vaughan (1918); van der Horst (1922a); Matthai (1924); Scheer (1967).

Lophoseris knorri Edwards & Haime, 1851a.

Of the above species of Dana, *Pavona formosa* is virtually identical to Figs. 8 and 13. The holotype has relatively thick broad fronds with centres arranged in regular rows. The columellae are well defined, the septa sub-equal. *Pavona praetorta* is almost certainly the same species (similar in growth form to Fig. 6). Another specimen of Dana's series (USNM 96) is approximately intermediate between *P. formosa* and *P. praetorta*. *Pavona venusta* was considered a separate species closely related to *P. praetorta* by Vaughan. However, fragments of the type have essentially similar septal structures to some specimens of the present series, with only six septa reaching the columellae.

Material studied

Darnley Island, Yorke Island (7 specimens), **Turtle Backed Island, Bewick Island** (3 specimens), **Lizard Island, Ribbon Reef** (2 specimens), plug reef S of **Ribbon Reef, Low Isles** (3 specimens), **Palm Islands** (57 specimens), **Pandora Reef, Bushy Island-Redbill Reef** (2 specimens), **Pompey Complex, Swain Reefs** (3 specimens).

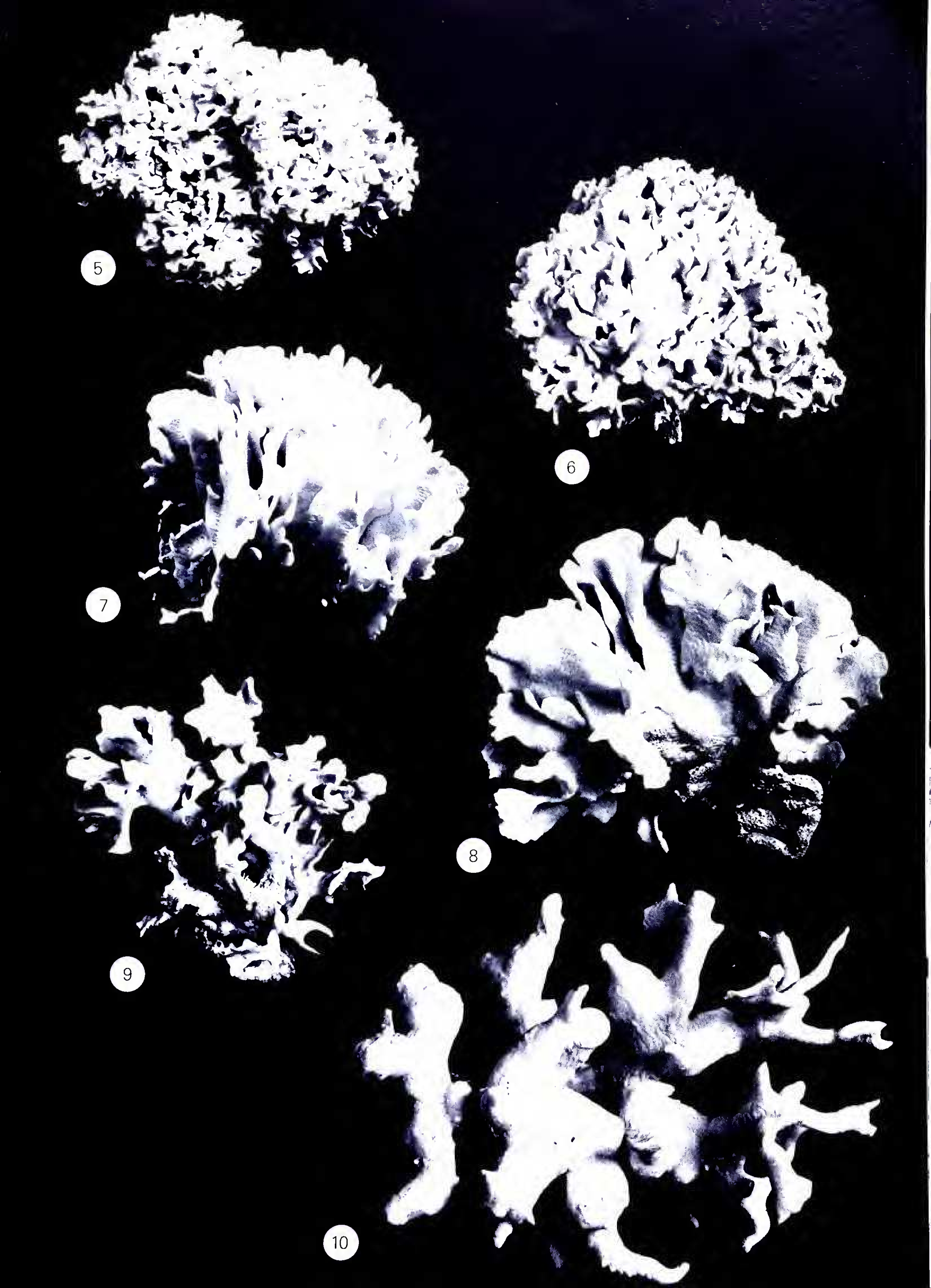
These localities include collecting stations 13, 33, 41, 42, 45, 55, 57, 59, 64, 65, 71, 73, 81, 90, 91, 92, 111, 125, 138.

Previous records from Eastern Australia

Low Isles, Stephenson & Stephenson (1933), Crossland (1952); **Batt Reef,** Crossland (1952).

Figs. 5-10 *Pavona cactus* (× 0.45).

Fig. 5 From Pioneer Bay, Orpheus Island, Palm Islands, collecting station 45.
Figs. 6-10 From Eclipse Island, Palm Islands, collecting station 59, showing growth form variation within a single large monospecific stand (× 0.45). Fig. 6, same corallum as Fig. 11, showing close similarity to the holotype of *P. praetorta*; Fig. 7, same corallum as Fig. 14; Fig. 8, same corallum as Fig. 13; Fig. 9, same corallum as Fig. 12; Fig. 10, showing thickening of branches of older parts of colony.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6
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Several references to *P. danai* by Crossland and Yonge also appear to refer to this species.

Characters

Pavona cactus is commonly found in protected or turbid waters where it frequently covers very extensive areas. Colonies consist of anastomosing fronds up to 30cm high with individual fronds commonly 4cm wide and 3-5mm thick. Fronds may be entire and flat and may be arranged parallel to each other, or may be twisted, divided and highly anastomosed. They are always bifacial with calices arranged in rows parallel to the margin. Calices are superficial, <5mm wide, and are widely separated. Sometimes carinae of irregular height are developed between them. Septo-costae are in regular straight rows perpendicular to the margin and plunge vertically into the calices and are thin and very heavily granulated, with smooth margins. They are in two alternating orders. Those of the first order, usually 6-8, reach the columella. They are slightly more exsert and more granulated than those of the second order. The columellae are frequently very poorly developed although they may be styliform or irregular in shape. In each case they can be seen to consist of a few fused trabeculae. There are no paliform lobes.

Living colonies (Fig. 730) usually have a pale uniform colour, usually brown.

Figs. 11-14. *Pavona cactus* from Eclipse Island, Palm Islands, collecting station 59.

Fig. 11 Same corallum as Fig. 6 (× 2.5).
Fig. 12 Same corallum as Fig. 9 (× 2.5).
Fig. 13 Same corallum as Fig. 8 showing close similarity with the holotype of *P. formosa* (× 4.2).
Fig. 14 Same corallum as Fig. 7 (× 7.8).

Fig. 11 ▼

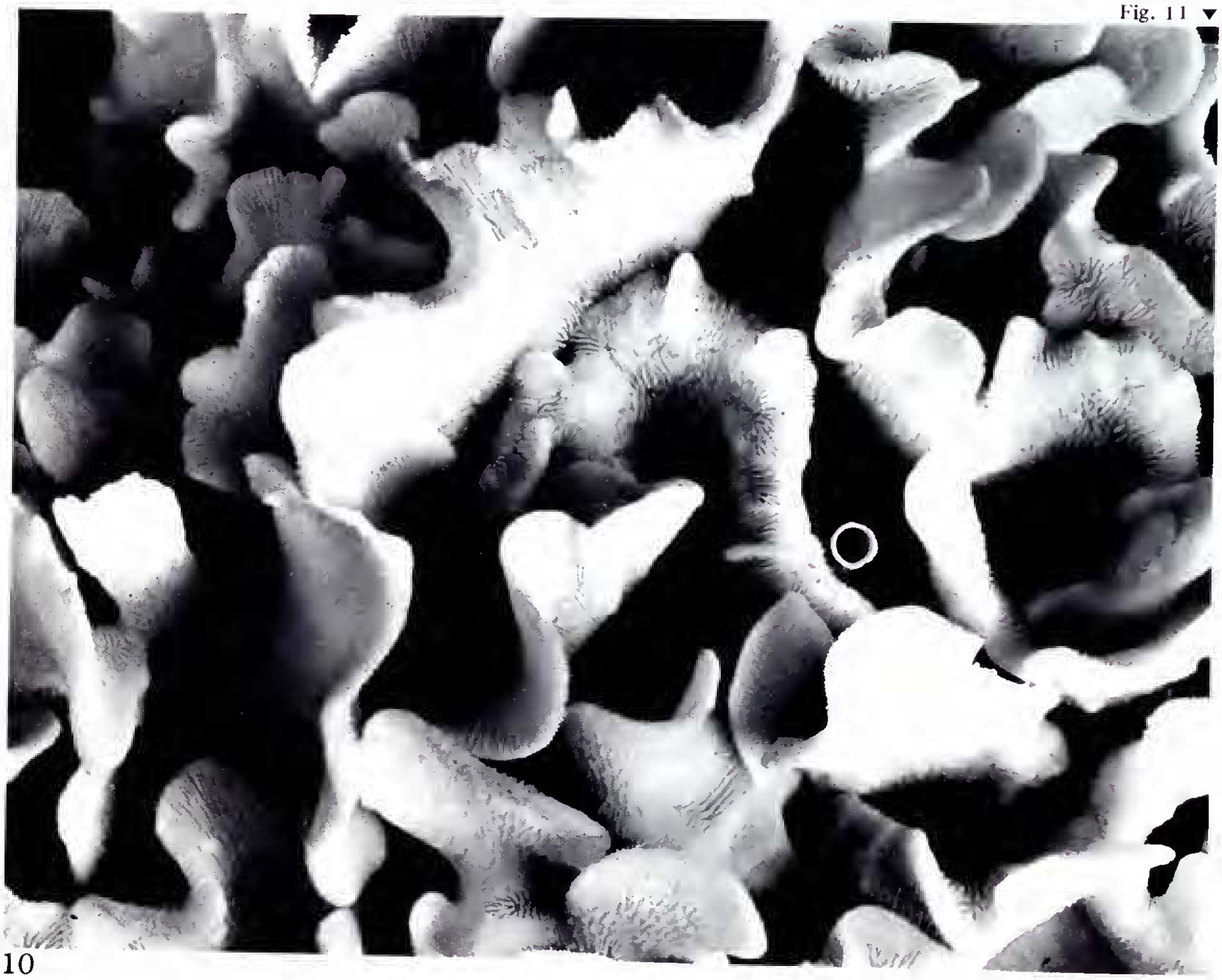

Fig. 12 ▲

Fig. 13 ▼

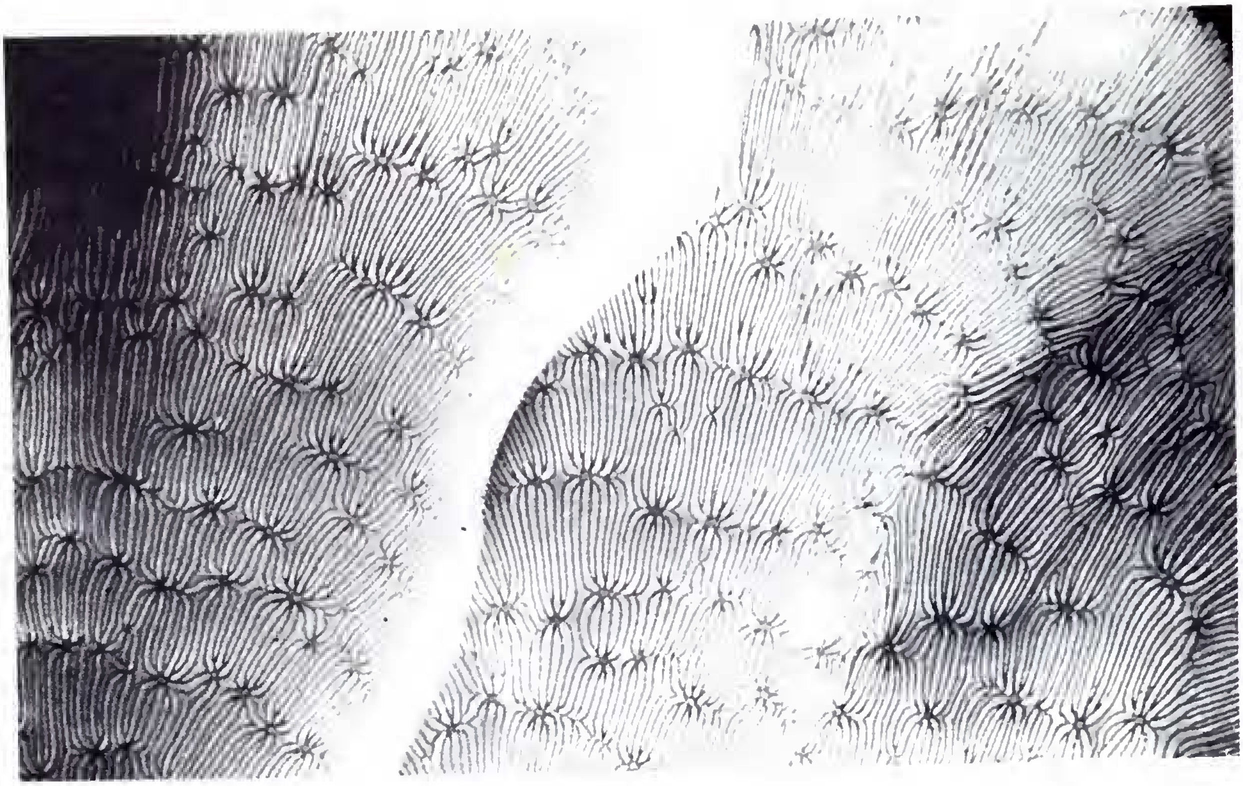

Fig. 14 ▲

Skeletal variation

Figures 6-10 illustrate the range of growth forms of *P. cactus* from a single large monospecific stand at Eclipse Island at 3-7m depth. Most of the growth form variation of the species can be found within such uniform biotopes, the difference between colonies or parts of colonies apparently being more a function of age rather than environmental conditions. Corallites are similar in all growth forms. They are always superficial and usually widely separated. They differ only in degree of calcification, which varies according to their position on branches.

Fig. 15 *Pavona cactus* from Swain Reefs, collecting station 69.

Distribution

Widely distributed throughout the tropical Indo-Pacific, from the Red Sea to the Marshall Islands.

Pavona decussata (Dana, 1846)

Synonymy

Pavonia decussata Dana, 1846; Quelch (1886); Bedot (1907).

Pavona decussata (Dana); van der Horst (1922a, 1922b); Matthai (1924, 1948c); Hoffmeister (1925); Faustino (1927); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1940); Crossland (1952); Stephenson & Wells (1955); Nemenzo (1955a); Utinomi (1965, 1971); Scheer (1967); Pillai & Scheer (1973).

Pavona crassa Dana, 1846.

Pavona lata Dana, 1846.

Pavona seriata Brüggemann, 1879b; Yabe, Sugiyama & Eguchi (1936).

Hoffmeister's (1925) assertion that *P. danai* belongs with *P. decussata* is not supported by the present study. Of the Dana species noted above, the holotype of *P. crassa* consists of a solid flat plate, a common growth form of *P. decussata* (Fig. 17). That of *P. lata* is also close to *P. decussata* (Fig. 21); the growth form is similar and calices are of similar size. However, *P. lata* has large dome-like columellae occupying most of the central space of the calices, which are not present in any Great Barrier Reef *P. decussata*. Both types are from Fiji.

The holotype of *P. seriata* is very similar in growth form to that of *P. decussata*. It differs in having larger columellae, although not as large as those of *P. lata*.

Material studied

Darnley Island, Yorke Island, Anchor Cay (4 specimens), **Warrior Reef, Aureed Island, Dungeness Island, Sue Island** (2 specimens), **Tijou Reef, Houghton Island, Nymph Island** (2 specimens), **MacGillivray Reef** (2 specimens), **Ribbon Reef, Hope Island** (2 specimens), **Low Isles, Palm Islands** (26 specimens), **Whitsunday Islands, Pompey Complex** (2 specimens), **Swain Reefs** (4 specimens), **Wistari Reef** (2 specimens).

These localities include collecting stations 2, 13, 17, 34, 36, 37, 39, 40, 41, 42, 43, 45, 59, 60, 65, 69, 72, 74, 79, 81, 87, 90, 91, 92, 97, 117, 121, 122, 125, 129, 133.

Previous records from Eastern Australia

Low Isles, Marshall & Stephenson (1933), Manton (1935), Moorhouse (1936), Crossland (1952), Stephenson & Wells (1955).

Figs. 16-18 *Pavona decussata* (× 0.33).

Figs. 16, 17 From Eclipse Island, Palm Islands, collecting station 59.
Fig. 18 From Nymph Island, collecting station 87, showing massive and frondose growth forms.

Figs. 19-24 *Pavona decussata* (× 5.0).

Fig. 19 From Eclipse Island, Palm Islands, collecting station 59.
Fig. 20 From Nymph Island, collecting station 87.
Fig. 21 From Low Isles, showing close similarity with the holotype of *P. lata*.
Fig. 22 From Eclipse Island, Palm Islands, collecting station 59.
Fig. 23 From Pioneer Bay, Orpheus Island, Palm Islands, collecting station 91.
Fig. 24 From Yorke Island, collecting station 13.

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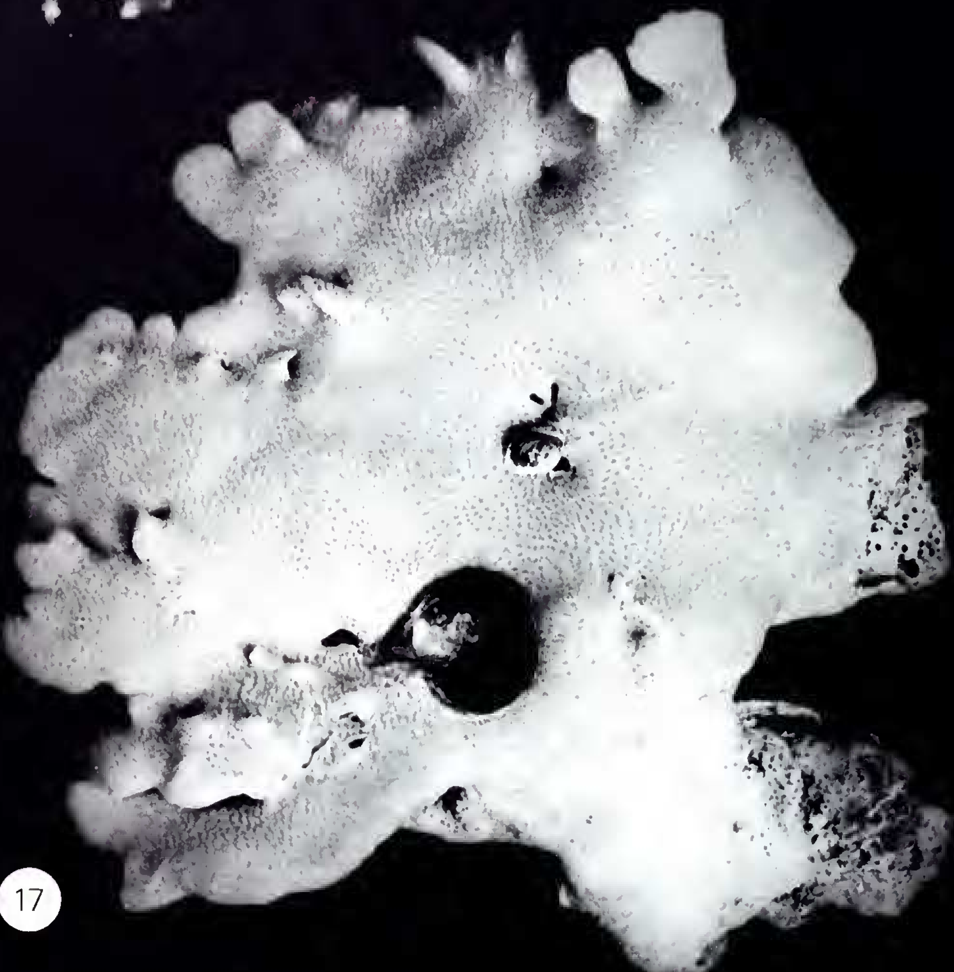

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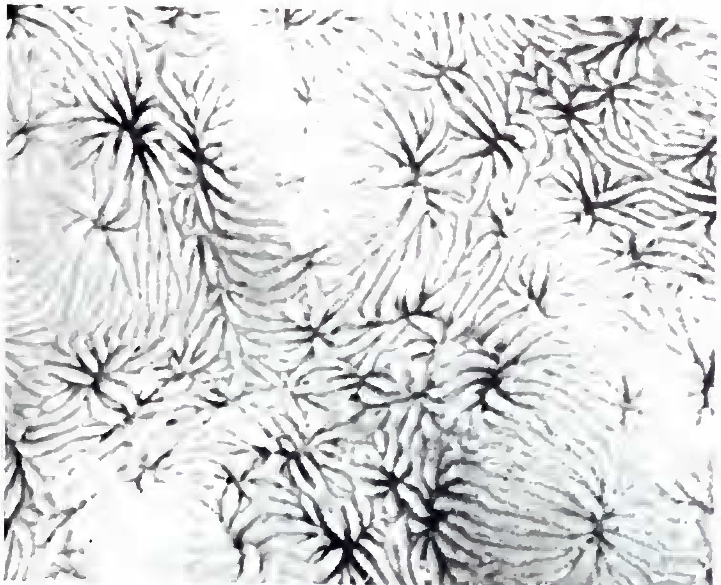


Fig. 19 ▲

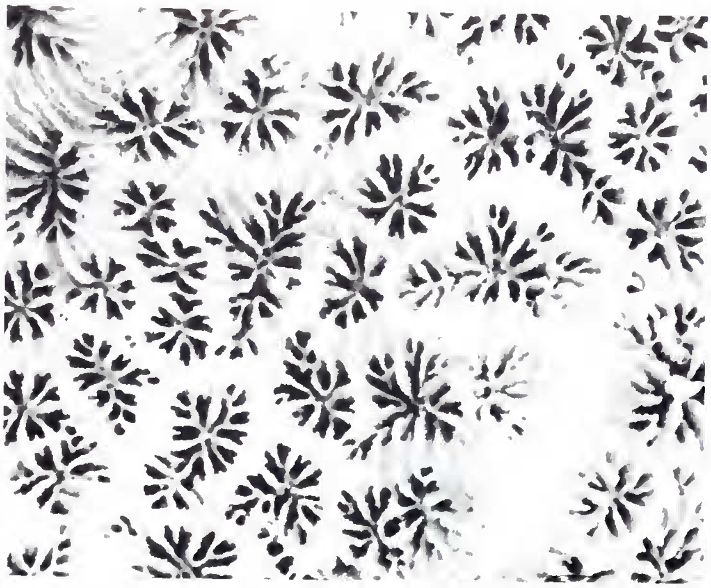


Fig. 20 ▲

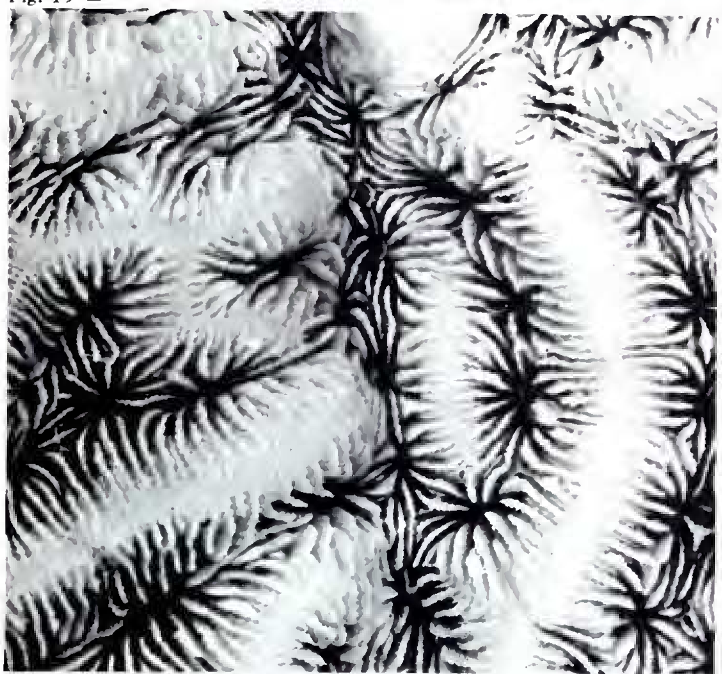


Fig. 21 ▲

Fig. 22 ▼

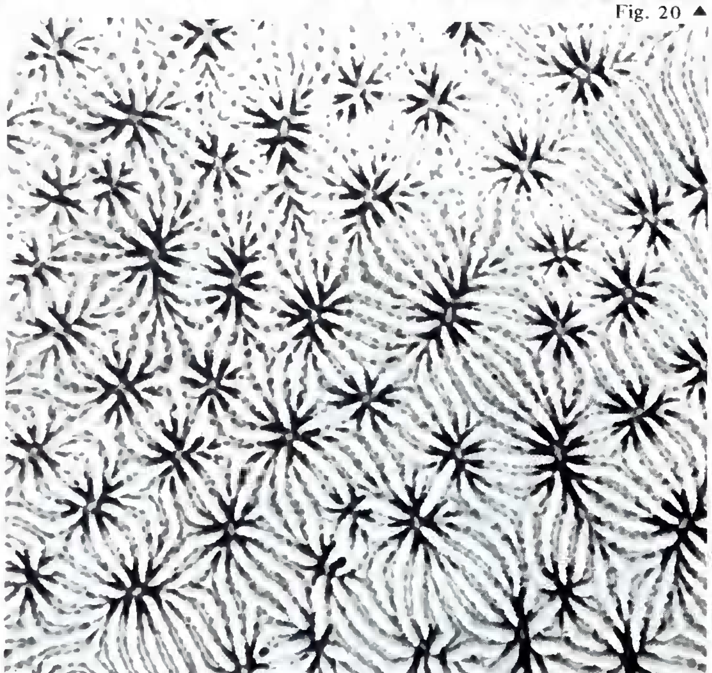
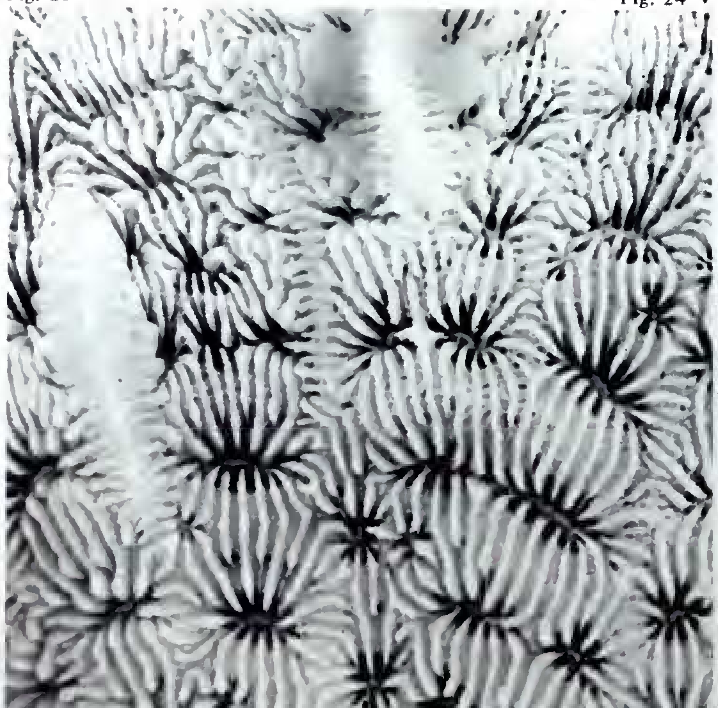


Fig. 23 ▲

Fig. 24 ▼



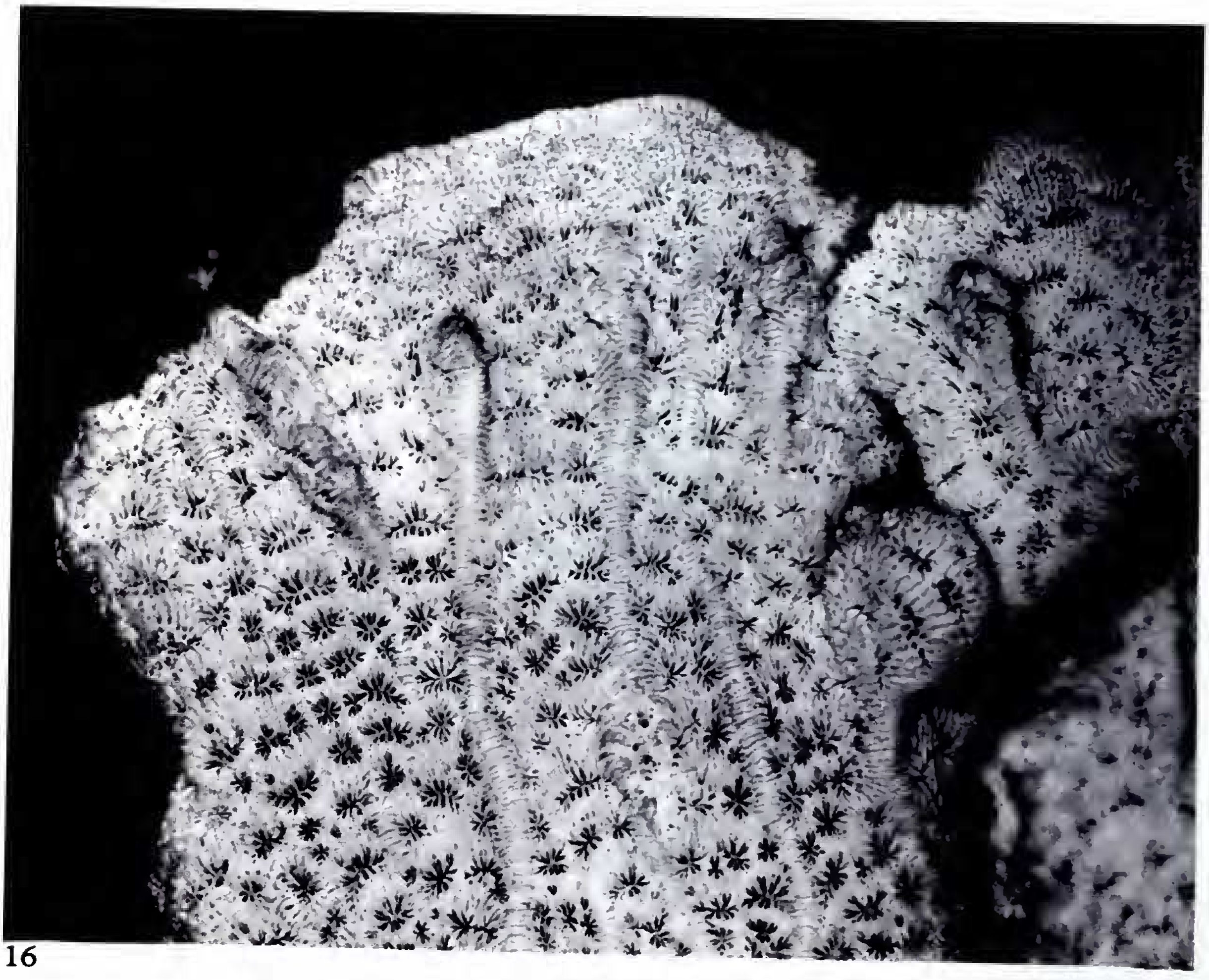
Characters

Colonies growing on a flat exposed substrate, especially where moving sand is abundant, are frequently flat or undulated, either encrusting or massive. At the other extreme, colonies may be composed wholly of vertical, anastomosing fronds (Fig. 731). Sometimes both massive and frondose growth forms are found in the same colony (Fig. 18). Fronds frequently grow to 6 cm in width and are usually approximately 6 mm thick at their centres. They have a wide variety of shapes but tend to grow vertically and have relatively straight upper margins. Fronds of many colonies have ridges running lengthwise along them which are free of corallites although seldom are these ridges as well developed as they are on the holotype (Fig. 25).

Fronds are always bifacial with calices irregularly distributed or arranged in short, irregular rows. Calices are approximately 3 × 1 mm and are very deep. Two cycles of septo-costae radiate from the calices with only a slight tendency to run perpendicular to the margin. First cycle septo-costae are thicker and far more exsert than those of the second cycle. They plunge vertically within the calices to anastomose and/or to fuse with the columellae. They are more heavily granulated than second cycle septo-costae, although the granulations are seldom as dense as in most *Pavona* species and septa are relatively widely separated. Second cycle septo-costae are thin, sparsely granulated, do not reach the columellae and are sometimes only discerned at the calice rim. Occasionally a septo-costa of one cycle changes into that of another. Columellae are poorly developed and always lie deeply within the calices. Usually they appear to consist of little more than fused first order septa.

Living colonies are usually creamy-yellow or greenish in colour.

Fig. 25 Holotype of *Pavona decussata* (× 1.5).



Affinities

This species does not closely resemble any others of the Great Barrier Reef. It is perhaps closest to *P. cactus*. Relationships with species not found on the Great Barrier Reef are mentioned above (p. 10).

Pavona cf. explanulata (Lamarck, 1816)

Synonymy

Agaricia explanulata Lamarck, 1816.

Pavona explanulata (Lamarck); Pillai & Scheer (1976).

Pavona maldivensis (Gardiner); *sensu* Vaughan (1918).

? *Leptoseris gravieri* van der Horst, 1922a.

This synonymy is far from complete as this species appears to have been referred to many times under different names. It has been clearly illustrated by Vaughan (1918) Pl. 56, Fig. 3a (as *P. maldivensis*) and Pillai & Scheer (1976) Pl. 16, Fig. 3 (as *P. explanulata*). The type specimen of *P. explanulata* has not been located in the Paris Museum. The name *explanulata* is used in the present account with reservations because the identity of this species has not been verified.

The type specimen of *L. gravieri* van der Horst appears to belong to the present species. This name was used by van der Horst for *L. incrustans* as the latter was pre-occupied by *Cylloseris* (= *Leptoseris*) *incrustans* Quelch (see p. 37), but the two species are distinct.

Figs. 26, 27 *Pavona* cf. *explanulata* (× 0.33).

Fig. 26 From Yorke Island, collecting station 126, showing maximum development of a columnar growth form.

Fig. 27 From Darnley Island, collecting station 31, showing an explanate growth form.

Figs. 28-33 *Pavona* cf. *explanulata*, Figs. 28-31 (× 5.0), Figs. 32, 33 (× 2.5).

Fig. 28 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.
Fig. 29 From Maer Island, Murray Islands, collecting station 26.
Fig. 30 From Yorke Island, collecting station 13.
Fig. 31 From Lord Howe Island.
Figs. 32, 33 From Darnley Island, collecting station 31.

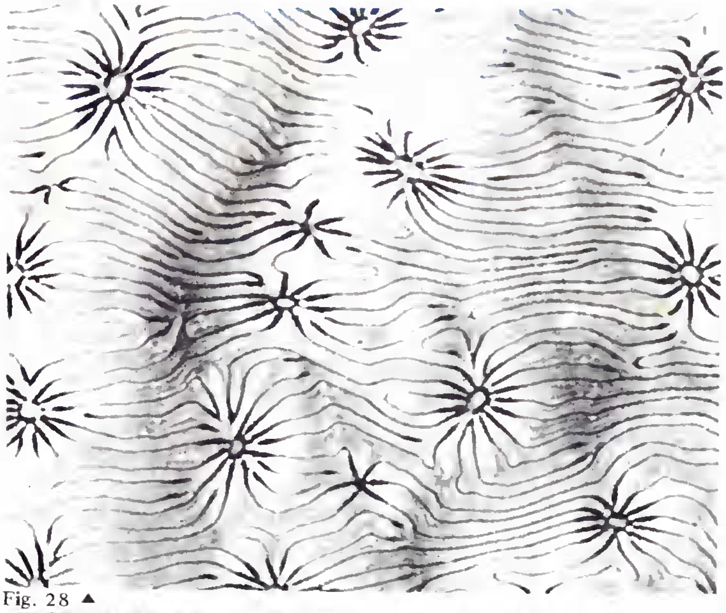


Fig. 28 ▲

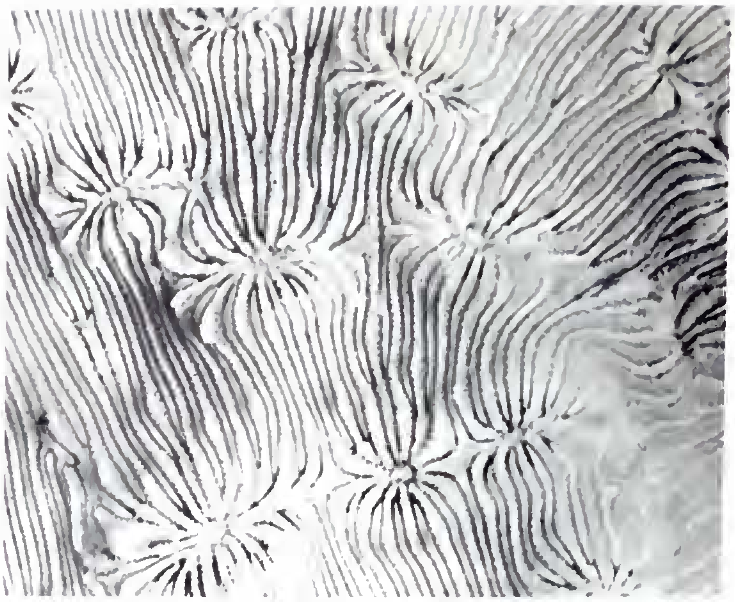


Fig. 29 ▲

Fig. 30 ▲

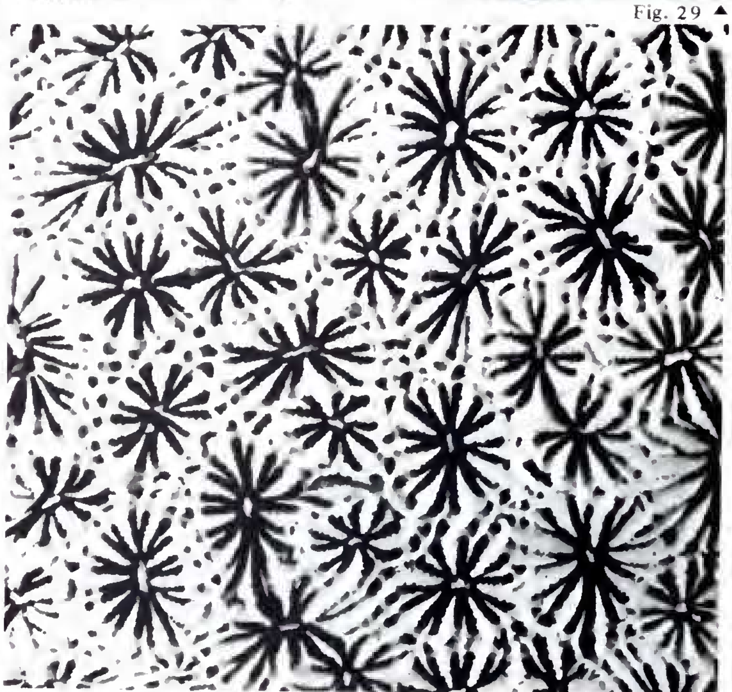


Fig. 31 ▲

Fig. 32 ▼

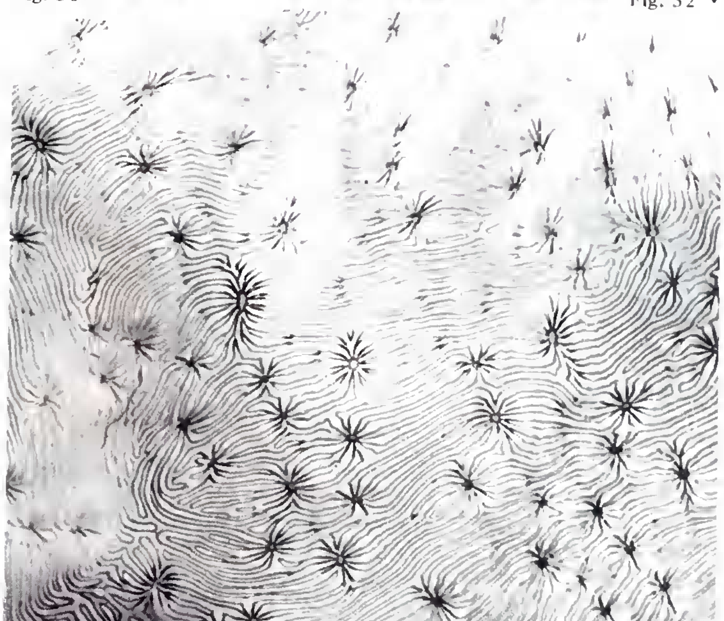


Fig. 33 ▼

Material studied

Bramble Cay (5 specimens), **Black Rocks, Darnley Island** (7 specimens), **Big Mary Reef, Yorke Island** (14 specimens), **Warrior Island, Murray Islands** (6 specimens), **Great Detached Reef, Jewell Reef** (2 specimens), **Lizard Island** (5 specimens), **Yonge Reef, Ribbon Reef** (3 specimens), **Palm Islands** (11 specimens), **Whitsunday Islands** (2 specimens), **Wistari Reef** (2 specimens), **Swain Reefs** (5 specimens), **Lord Howe Island** (3 specimens).

These localities include collecting stations, 1, 3, 13, 26, 27, 28, 29, 32, 33, 36, 45, 56, 63, 65, 77, 79, 81, 90, 98, 100, 117, 121, 125, 126, 127, 128, 131, 143, 147.

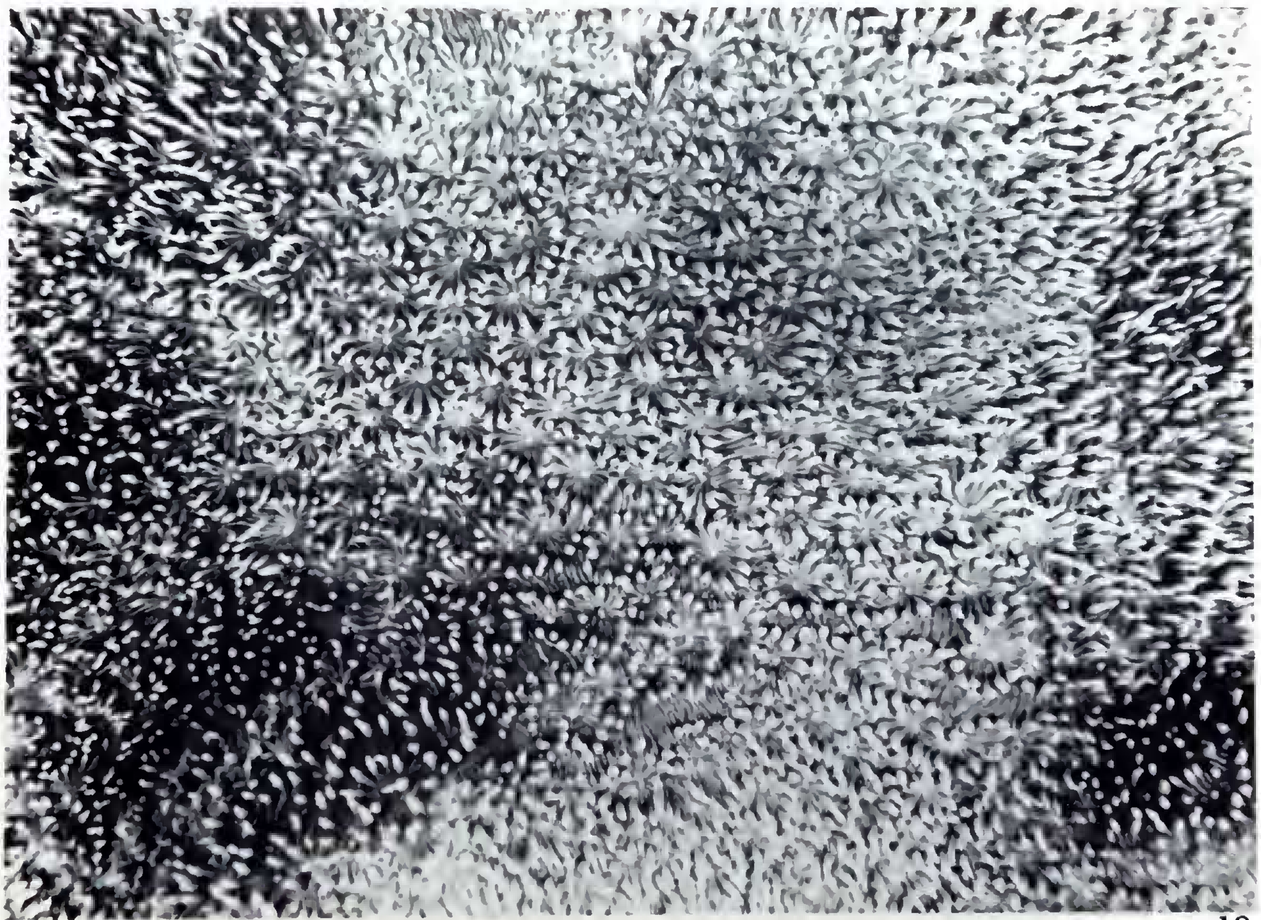
Previous records from Eastern Australia

Lord Howe Island, Veron & Done (1979).

Characters

Colonies are primarily encrusting or laminar. Larger colonies have a tendency to become massive, plate-like or columnar (Fig. 26). Mature corallites vary in size from 3.5-6.5 mm diameter. They are arranged irregularly, or , in some laminar coralla, tend to be arranged in rows parallel to the margin. Irregular corallites are radially symmetrical, while laminar corallites are inclined towards the margin. Corallites have deep, well defined fossae largely filled with septa of two very distinct orders. First order septa are usually very exsert, thinner than second order septa, and much more granulated. Second order septo-costae usually have smooth margins. All septo-costae are closely packed; they frequently branch to three or more corallites and are often crenellated. Towards the margins the septo-costae are fine and straight and have few granulations. In some coralla there are irregular lobes on the costae usually associated with free margins and alveoli. The columellae usually consist of a few fused, twisted

Fig. 34 *Pavona* cf. *explanulata* from Lord Howe Island, collecting station 147.



trabeculae, which frequently form a conspicuous pillar. The thecae are primarily synapticulothecate or completely absent; individual synapticulae are frequently visible in immature corallites. Budding may be both intra- and extra-tentacular.

Living colonies (Figs. 732, 733) may have a wide variety of colours. The majority are various shades of grey, but some are brown, pink, purple or yellow. Some colonies have uniform colours, some are mottled, others have different coloured coenosteum and corallites.

Skeletal variation

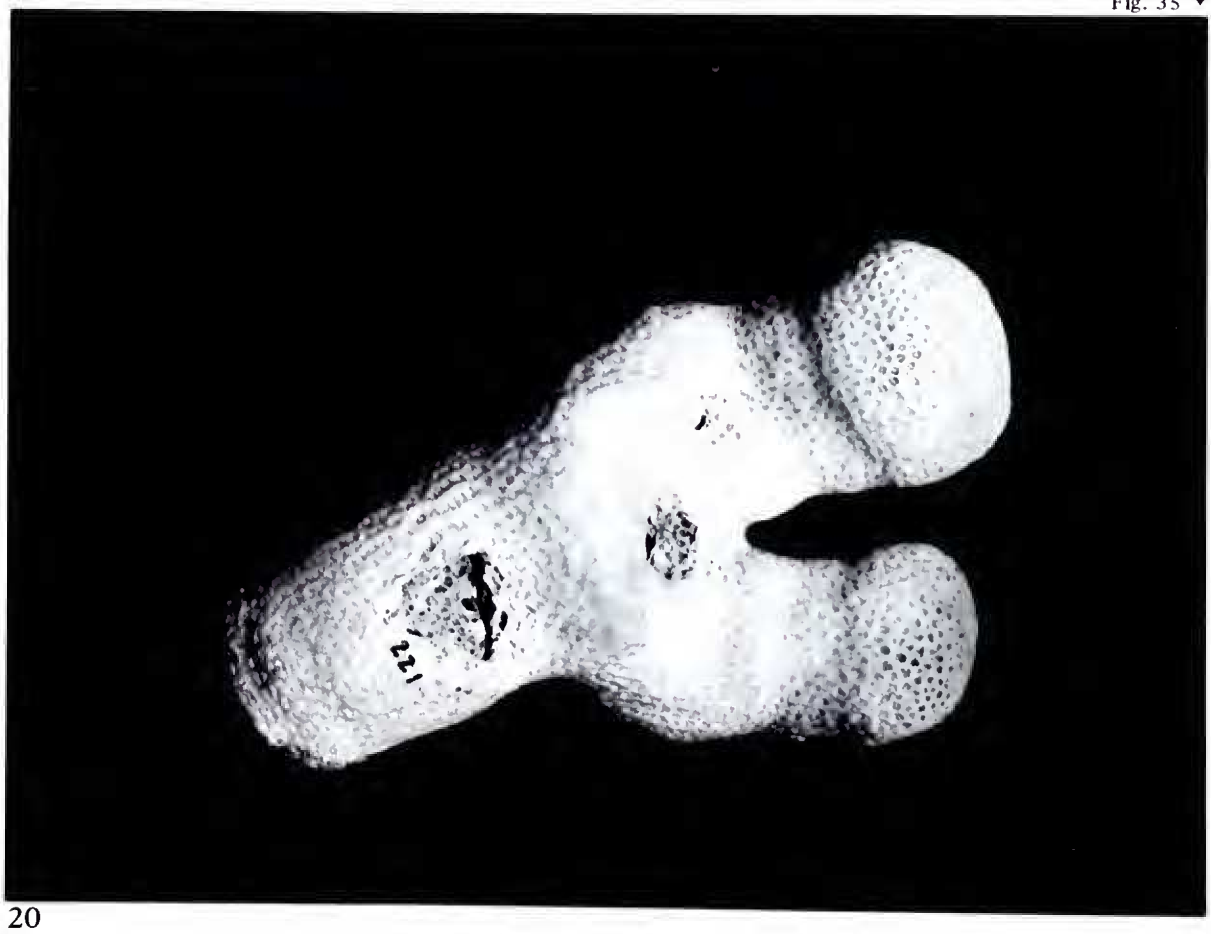
Colonies from shallow water exposed to strong light and turbulence are usually massive or sub-massive. In very exposed conditions such colonies may develop columnar extensions. All coralla from such biotopes have closely packed, largely cerioid corallites which are mostly symmetrical. Colonies from deeper water are plate-like with thin laminar margins with usually plocoid corallites. Those from the deepest limits of coral growth (e.g. the type of *L. gravieri* from '>25 fms.') are encrusting and consist entirely of thin, unifacial laminae with relatively superficial corallites.

Affinities

The generic affinities of *P. explanulata* are far from clear. Massive coralla, or the central areas of plate-like coralla, usually have compact corallites very similar in structure (although not in size) to those of *P. minuta*. They mostly lack any form of a corallite wall as do most *Pavona* species. However, the margins of such coralla, as well as most of the area of encrusting coralla are usually thin, unifacial laminae with widely spaced corallites similar to, although readily distinguished from, those of *L. hawaiiensis* and *L. explanulata*. On a specific level, *P. explanulata* is readily distinguished from other east Australian *Pavona* and *Leptoseris* species. Its wide variation

Figs. 35, 36 Holotype of *Pavona clavus* Fig. 35 (× 0.8), Fig. 36 (× 5.0).

Fig. 35 ▼



and consequent uncertain generic position reflects doubt on the usefulness of separating these genera, rather than on the validity of *P. explanulata* as a single discrete species.

Distribution

Confirmed records of this species are from Madagascar, the Amirante Islands (type locality of *L. gravieri*); and the Cocos-Keeling Islands in the Indian Ocean and now the Great Barrier Reef and Lord Howe Island in the Pacific.

Pavona clavus (Dana, 1846)

Synonymy (partly after van der Horst, 1922a)

Agaricia clavus Dana, 1846.

Lophoseris clavus (Dana); Edwards & Haime (1860).

Siderastrea clavus (Dana); Verrill (1864).

Siderastrea sphaeroidalis Ortmann, 1889.

Tichoseris clavus (Dana); Rehberg (1892).

Pavona clavus (Dana); von Marenzeller (1901); van der Horst (1922a); Crossland (1935); Wells (1954); Ma (1959); Scheer (1964a); Pichon (1964); Chevalier (1968); Rosen (1971); *non* Scheer & Pillai (1974).

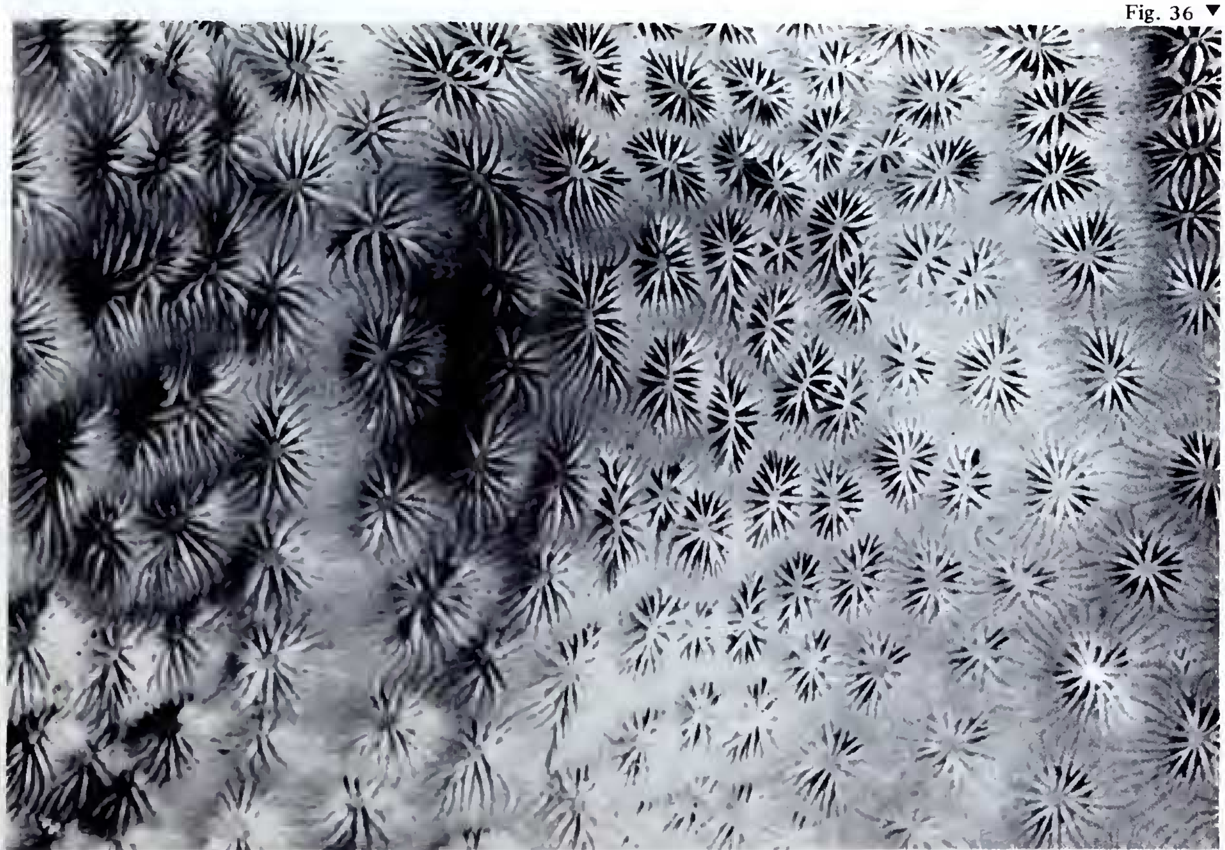
Pavona duerdeni Vaughan, 1907a; Crossland (1952); *non* Scheer & Pillai (1974).

Pavona lilacea (Klunzinger); *sensu* Yabe, Sugiyama & Eguchi (1936).

Pavona maldivensis (Gardiner); *sensu* Scheer & Pillai (1974), Pillai & Scheer (1976).

The holotype of *P. clavus* (Figs. 35, 36) has well defined sub-circular corallites separated by several rows of synapticular rings. *Pavona duerdeni* has smaller, less rounded corallites which are not as clearly separated as those of *P. clavus* and the columellae are less well developed. *Pavona clivosa* is very close to *P. clavus* with corallites of similar size although less calcified and set closer together.

Fig. 36 ▼



The synonymy of *P. clavus* has been discussed at some length by van der Horst (1922a). His inclusion of *P. duerdeni* in it was supported by Wells (1954). However, as noted by Crossland (1952), his inclusion of *P. maldivensis* in *P. clavus* is incorrect.

Material studied

Bramble Cay, Black Rocks (3 specimens), **Yorke Island** (4 specimens), **Warrior Reef, Dungeness Island** (7 specimens), **Big Mary Reef** (2 specimens), **Newman Reef,** plug reef S of **Ribbon Reef** (4 specimens), **Palm Islands** (3 specimens).

These localities include collecting stations 13, 35, 43, 64, 91, 121, 122, 126, 127, 128, 131, 134.

Fig. 37 *Pavona clavus* from a plug reef S of Ribbon Reef, collecting station 64.

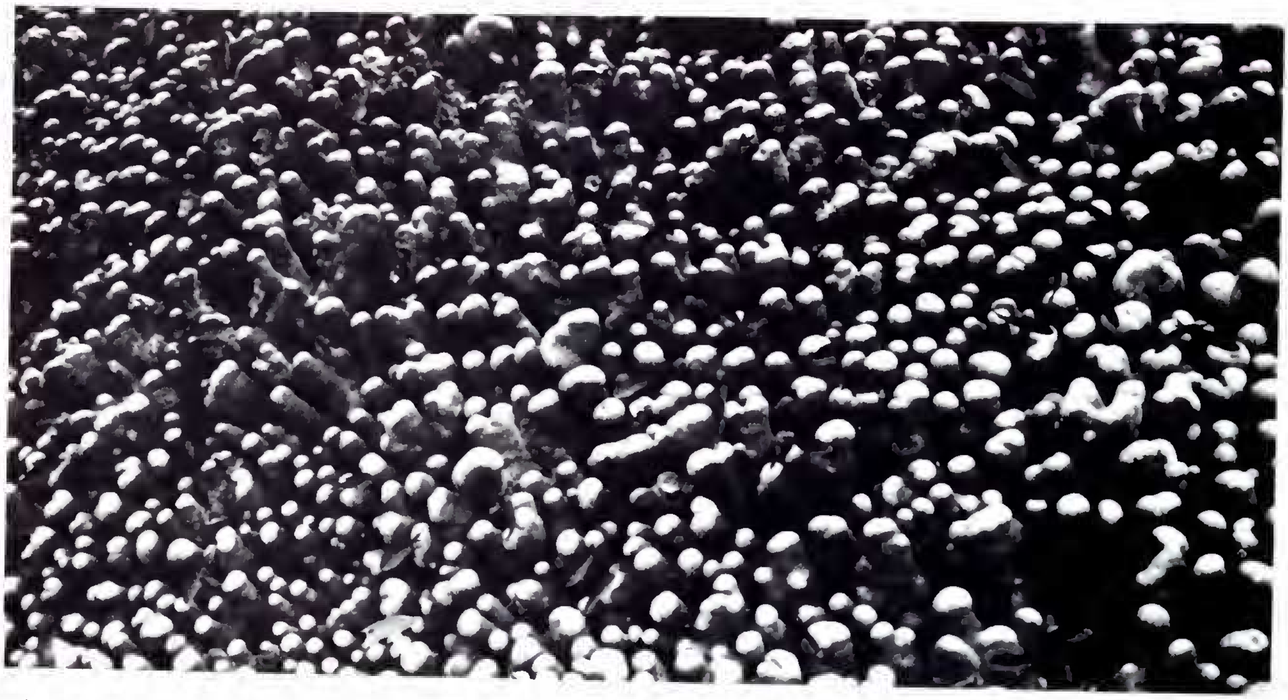


Fig. 38 *Pavona clavus* from a plug reef S of Ribbon Reef, collecting station 64, showing part of the colony illustrated in Fig. 37 (× 0.5).

Previous records from Eastern Australia

Great Barrier Reef (as *P. duerdeni*), Crossland (1952).

Characters

Small colonies may be encrusting to massive, rarely laminar (Fig. 734). Larger colonies are mostly clavate or columnar with columns up to 10 cm thick, circular or elliptical in sections, and up to 1.5 m high. In ideal conditions of clear water with a good circulation but protection from strong wave action, individual colonies may exceed 20 m in diameter (Fig. 37).

Figs. 39, 40 *Pavona clavus* (× 5.0).

Fig. 39 From a plug reef S of Ribbon Reef, collecting station 64, showing close similarity with the holotype (Figs. 35, 36).

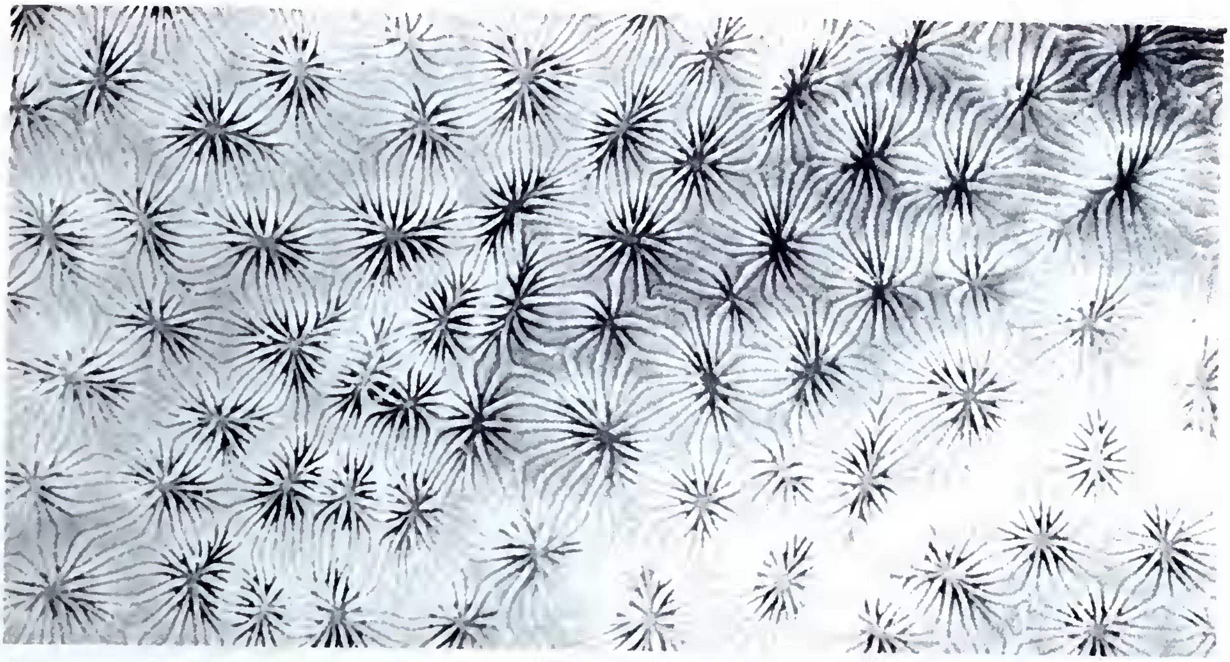


Fig. 40 From Bait Reef.

Mature calices are 2.5-3.5 mm in diameter and are irregularly arranged or are aligned in short shallow valleys. In the latter case, adjacent corallites may be separated by as little as two common septa with almost no development of a theca. Usually the thecae are thick and sometimes form low carinae. Septo-costae are clearly arranged in two alternate orders, usually 6-13, but sometimes as many as 20 each. First order septo-costae are thinner and reach the columellae. All septa slope evenly or sometimes unevenly into the calices and usually have steeply sloping inner margins. All septo-costae are closely packed and are usually very thick and straight. They have smooth margins and granulated sides. First order septa frequently anastomose and all fuse at the bottom of the calice centres. Columellae are rudimentary, or absent.

Figs. 41-44 *Pavona minuta* (× 5.0).

Fig. 41 From Maer Island, Murray Islands, collecting station 27.
Fig. 42 From Wistari Reef.
Fig. 43 From Lord Howe Island.
Fig. 44 From a plug reef S of Ribbon Reef, collecting station 64.

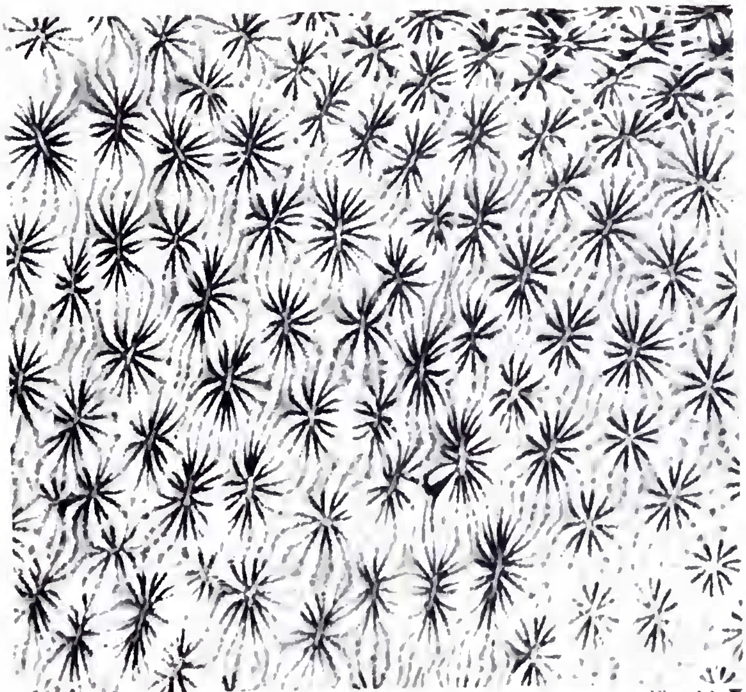


Fig. 41 ▲

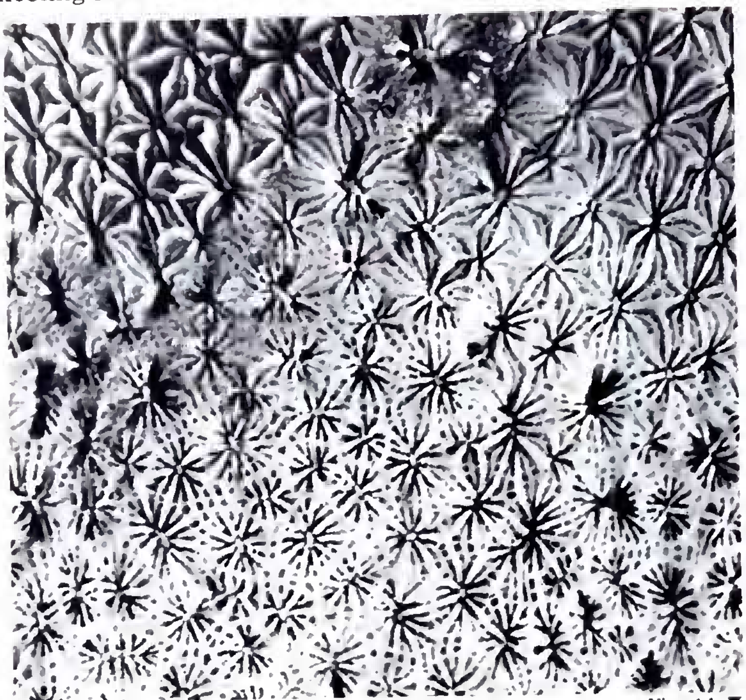


Fig. 42 ▲

Fig. 43 ▼

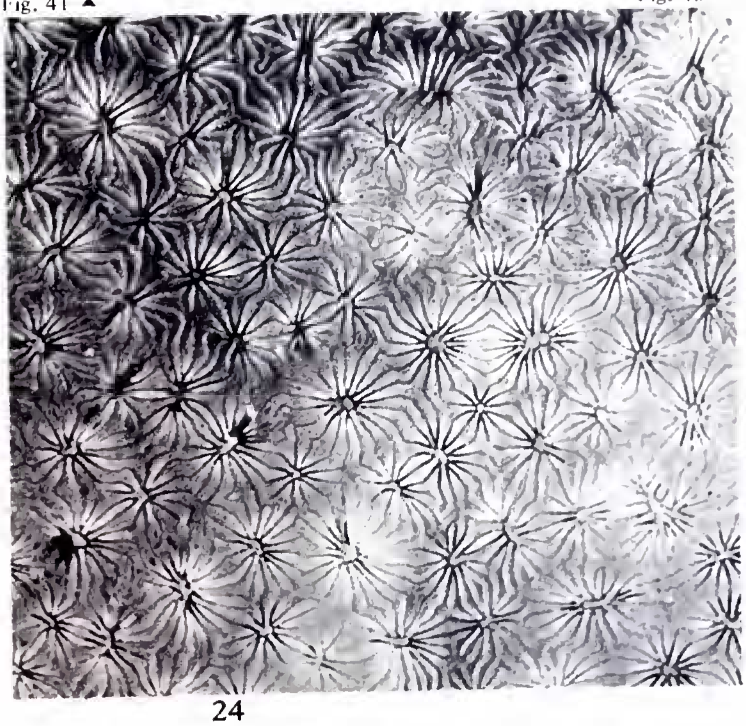
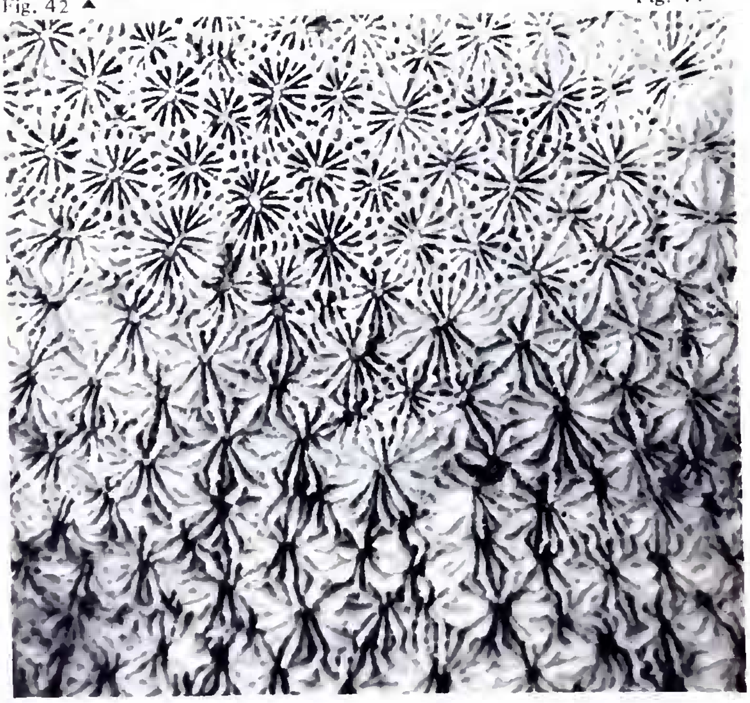


Fig. 44 ▼



Colonies are usually a uniform pale grey or brown in colour.

Affinities

Both Vaughan (1918) and van der Horst (1922a) considered this species synonymous with *P. maldivensis*. The present series resembles only *P. minuta* from which they are clearly distinguished (see p. 26).

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea and the Mascarene Archipelago (Faure, 1976) in the west to the Marshall Islands, Fiji and Hawaii in the east.

Pavona minuta Wells, 1954

Synonymy

Pavona minuta Wells, 1954.

Pavona clavus (Dana); *sensu* Scheer & Pillai (1974).

Scheer & Pillai (1974) clearly illustrate this species (as *P. clavus*) Pl. 13, Figs. 1, 2.

Material studied

Bramble Cay (5 specimens), **Yorke Island** (3 specimens), **Murray Islands, Lizard Island, Yonge Reef,** plug reef S of **Ribbon Reef, Palm Islands, Lodestone Reef, Swain Reefs** (2 specimens), **Wistari Reef, Lord Howe Island.**

These localities include collecting stations 9, 27, 64, 81, 83, 117, 125, 128, 147.

Previous records from Eastern Australia

Lord Howe Island, Veron & Done (1979).

Characters

Colonies are massive with smooth undulating surfaces (Figs. 45, 46). They frequently attain very large sizes with a wide variety of growth forms from tall columns to flat plates, the latter frequently traversed with ridges of various shapes

Figs. 45, 46 *Pavona minuta* from Heron Island.

Fig. 45 ▼

Fig. 46 ▼

usually running perpendicular to prevailing currents. Calices are cerioid, 2-3 mm diameter and very regularly spaced, with centres 2.5-3 mm apart. Septo-costae are arranged in 2 alternate orders of 8-10 each. Those of the same order are continuous between adjacent corallites; some branch to reach 3, occasionally 4, different calices. They are closely packed and wedge-shaped and hence are thickest between corallites. Their sides are thickly granulated; their margins smooth and straight. There are no paliform lobes, the inner margins of the septa plunge steeply within the calices and are sometimes linked with a deep synapticular ring. The columellae are solid and made up of fused trabeculae. The thecae are made up of one or more synapticular, secondarily thickened rings.

Affinities

The growth form of this species may sometimes be similar to that of *P. clavus* which also has small calices. However, calicular structures are substantially different (compare Figs. 38 and 44 from adjacent colonies); *P. minuta* has more regular calices with fewer, more regular, more exsert septa and well formed columellae. Wells (1954) noted that *P. explanulata* and *P. diffluens* may have have a similar (encrusting) growth form.

Pavona xarifae Scheer & Pillai (1974), described from a single specimen (which has not been examined by the authors), appears to be very close to *P. minuta*.

Distribution

This species has previously been recorded only from the type locality, Bikini Atoll, Marshall Islands and the Nicobar Islands.

Pavona varians Verrill, 1864

Synonymy (partly after Vaughan, 1918).

Pavona varians Verrill, 1864; Vaughan (1907a, 1918) (*pars*); van der Horst (1921, 1922a); Matthai (1923a, 1924, 1948a, 1948b, 1948c); Yabe & Sugiyama (1935a); Crossland (1935, 1952); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Umbgrove (1940); Wells (1954); Stephenson & Wells (1955); Nemenzo (1955a); Ma (1959); Durham (1962); Pichon (1964); Scheer (1967, 1972); Pillai & Scheer (1974).

Lophoseris repens Brüggemann, 1877a; Ortmann (1888, 1889).

Pavona repens (Brüggemann); Klunzinger, 1879; Gardiner (1898, 1905); Whitelegge (1898); van der Horst (1922a).

Pavona percarinata Ridley, 1883.

Pavonia intermedia Gardiner, 1898; van der Horst (1922a); Chevalier (1968).

Van der Horst (1922a) included Gardiner's *P. calcifera* in the synonymy of this species. It is, however, a synonym of *P. venosa*.

Material studied

Pearce Cay, Yorke Island, Warrior Island, Dungeness Island, Murray Islands (3 specimens), **Great Detached Reef, Tijou Reef** (4 specimens), **Jewell Reef** (8

Figs. 47-52 *Pavona varians*, Figs. 47-51 (× 2.5).

Fig. 47 From the Swain Reefs, collecting station 67, showing high, convoluted collines.
Fig. 48 From the Swain Reefs, collecting station 79, showing development of valleys.
Fig. 49 From Lord Howe Island, collecting station 147.
Fig. 50 From Dewar Island, Murray Islands, collecting station 28.
Fig. 51 From Jewell Reef, collecting station 61.
Fig. 52 From Ashmore Reef, collecting station 107, showing extreme reduction of the collines associated with small calices (× 2.0).

Fig. 47 ▲

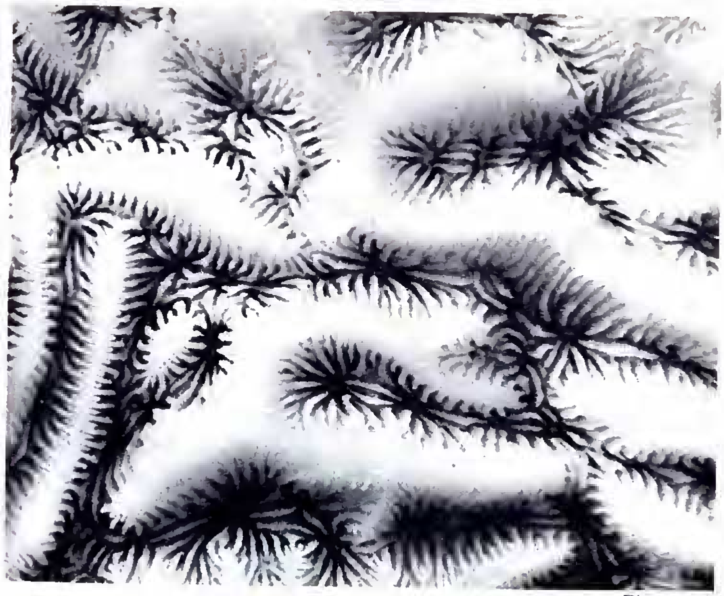


Fig. 48 ▲

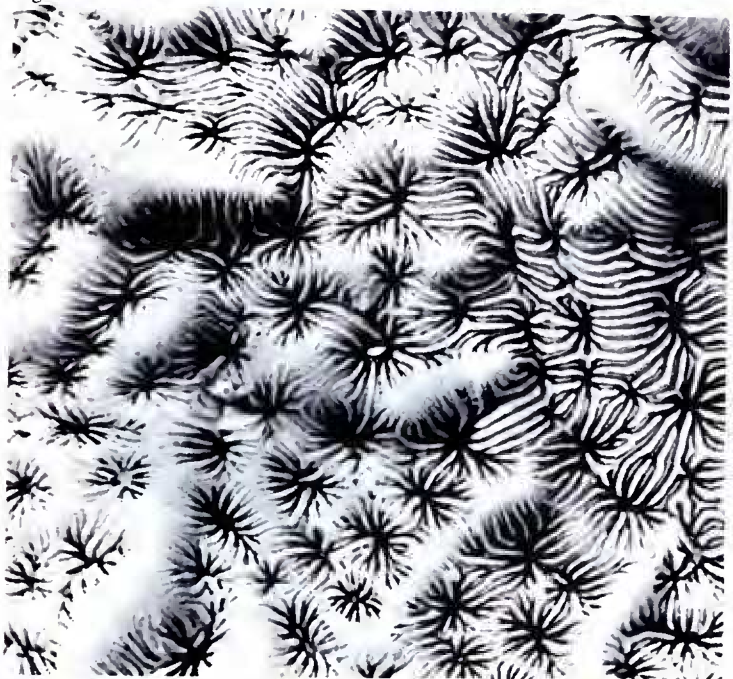


Fig. 49 ▲

Fig. 50 ▲

Fig. 51 ▼

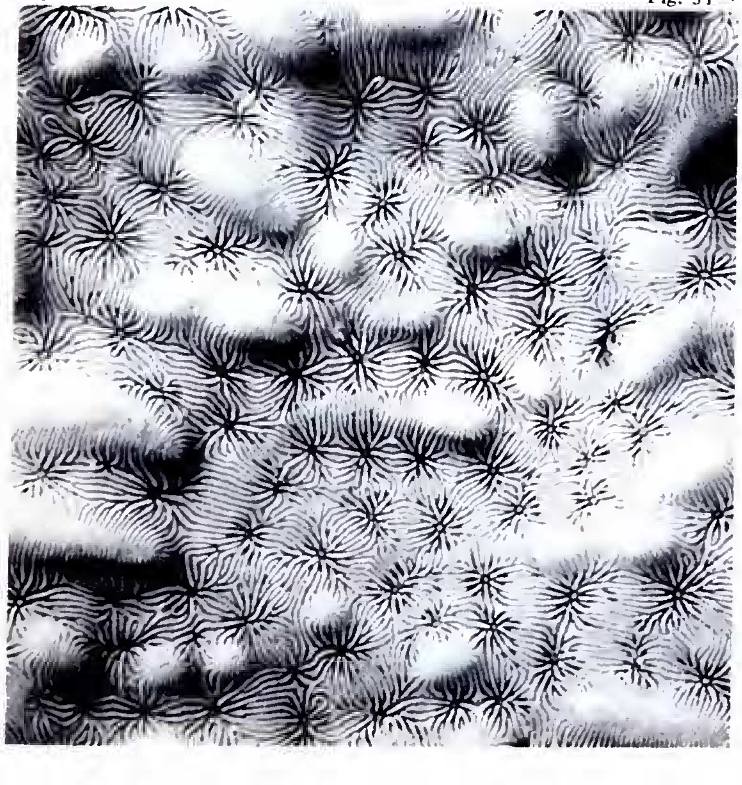
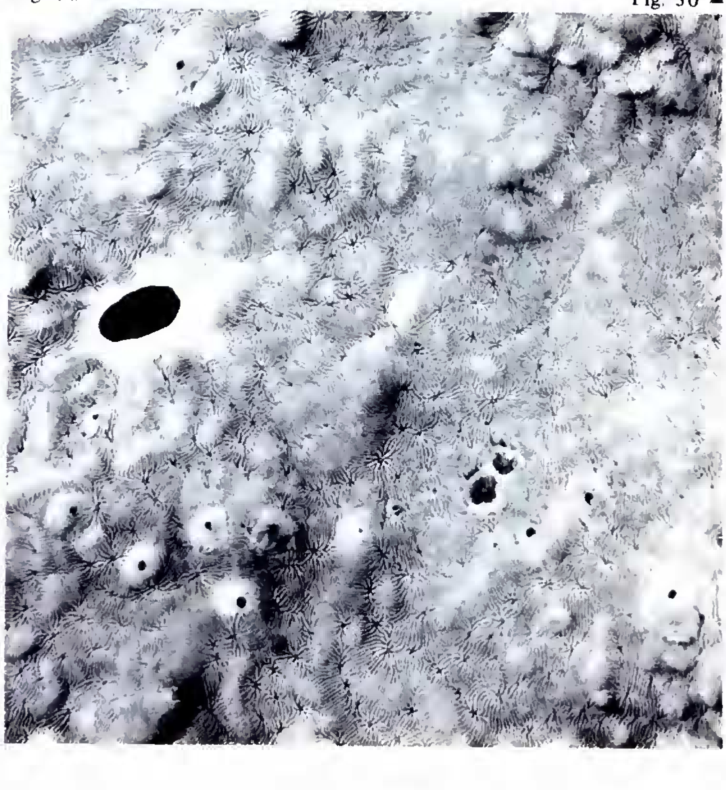


Fig. 52 ▼



specimens), **Lizard Island** (4 specimens), **Yonge Reef, Ribbon Reef** (3 specimens), plug reef S of **Ribbon Reef** (3 specimens), **Eyrie Reef, Palm Islands** (9 specimens), **Whitsunday Islands, Bushy Islands—Redbill Reef, Swain Reefs** (10 specimens), **Wistari Reef, Heron Island, Lord Howe Island** (3 specimens).

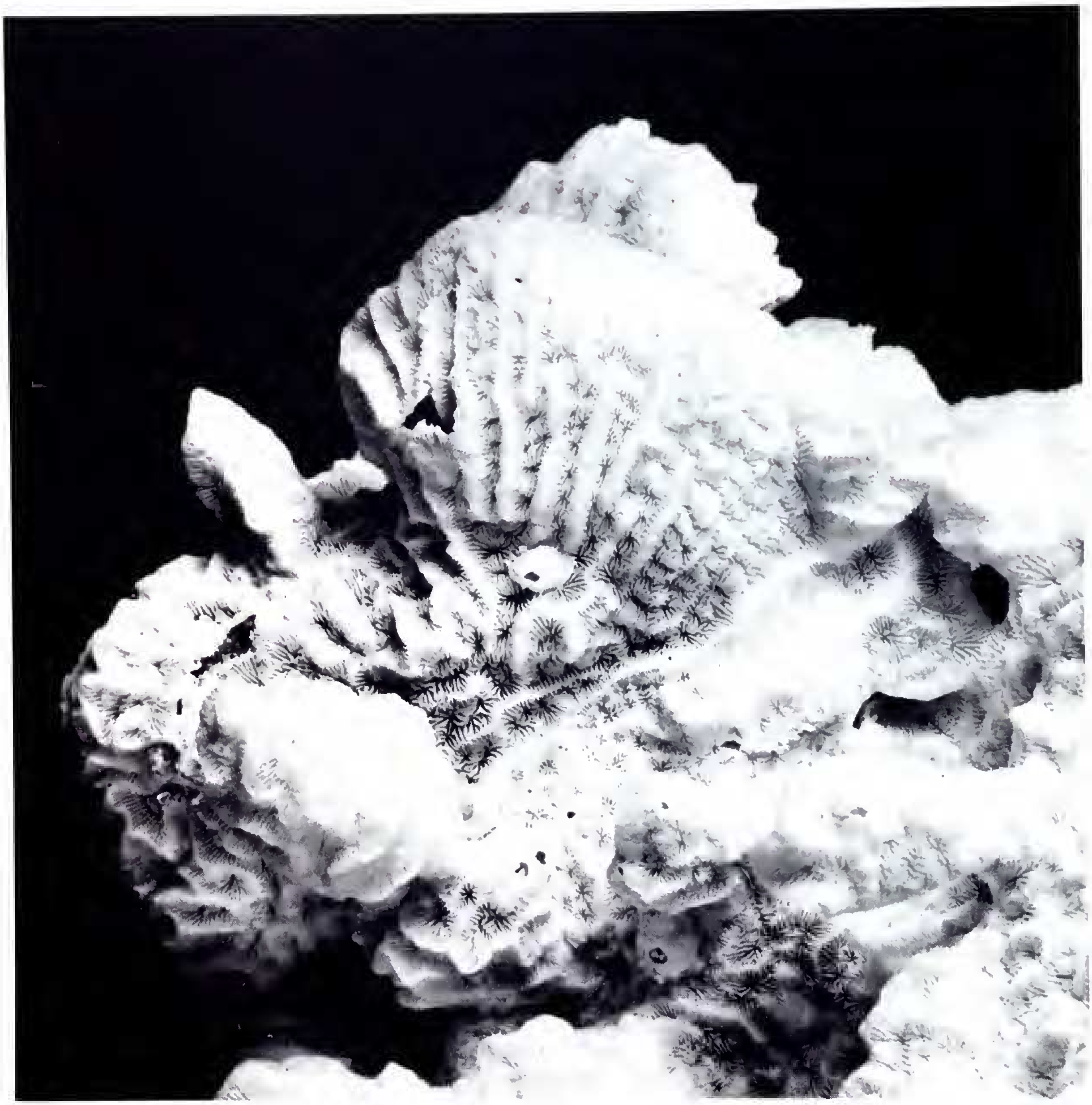
These localities include collecting stations 1, 2, 9, 19, 28, 30, 32, 33, 36, 37, 41, 55, 57, 58, 59, 61, 64, 65, 69, 76, 77, 79, 80, 81, 90, 91, 92, 98, 99, 117, 120, 121, 123, 124, 125, 126, 147.

Previous records from Eastern Australia

Murray Islands, Vaughan (*pars*) (1918), Mayor (1918), **Low Isles,** Crossland (*pars*) (1952), Stephenson & Wells (1955); **Fitzroy Island,** Stephenson & Wells (1955); **Lady Elliott Island,** Stephenson & Wells (1955).

As noted by Stephenson & Wells (1955), both Vaughan (1918) and Crossland (1952) confuse or partly confuse *P. varians* with *P. venosa.*

Fig. 53 *Pavona varians* from Dungeness Reef, collecting station 122, showing strongly developed radiating collines (× 2.0).



Characters

Colonies are encrusting, massive or laminar. Massive forms usually have an irregular shape; sometimes they occur as thick columns mostly adjoined to each other (Fig. 54). Laminar colonies, which develop under overhangs, are usually thin and flat. All colonies have an irregular surface covered with low, irregular collines. Sometimes these collines are long and straight, running perpendicular to the margin (Fig. 53); usually they are sinuous and irregular in length and direction. In parts of some coralla the collines are so short and irregular that they have the form of conical monticules. Corallites are distributed irregularly between the collines, either in rows or clusters. Sometimes they are linked together to form short valleys; usually they are discrete, with 1-6 laminar linkages between them. Calices are very small (1 mm maximum dimension) and are mostly filled by the septa and columellae. Septo-costae are arranged in two alternate orders which are indistinct in some coralla. Those of the first order are slightly thicker and more exsert; an average of 8 per calice reaches the columella. Many second order septo-costae do not extend inwards further than the bottom of the collines. Both orders are equally finely granulated. The shape of the columella varies greatly from a small, low boss, to a high plate-like structure hardly distinguishable from a laminar linkage. The undersurfaces of laminar colonies are smooth or finely costate and usually slightly undulating, the undulations corresponding to the collines of the upper surface.

The colour of individual colonies (Fig. 735) is frequently very variable, many having pale tops and dark sides. The most common colours are yellow, green and brown.

Fig. 54 *Pavona varians* from a plug reef S of Ribbon Reef, collecting station 64.

Skeletal variations

This species is aptly named as both the growth form and the fine skeletal structures vary greatly with environmental conditions. Unlike most Agariciidae, *P. varians* occupies a wide variety of biotopes. Coralla from exposed biotopes are almost always massive and have low, flat collines with relatively deep, widely spaced, calices. With increasing protection from wave action, collines become increasingly acute and laminar growth-forms develop. In the latter case, the collines may become arranged in near parallel rows with the corallites aligned accordingly. These combinations of characters are not always clear, however, and frequently considerable variation is found within the one corallum.

Affinities

As noted below, this species is very close to *P. venosa*. The latter is distinguished by its high sharp collines, the presence of three orders of septa, and the lack of columella development. Usually the septa are more widely spaced and less even in height.

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea to the Bonin Islands, Hawaii and Tahiti.

Pavona venosa (Ehrenberg, 1834)

Synonymy

Polyastra venosa Ehrenberg, 1834.

Pavonia calcifera Gardiner, 1898.

Tichoseris obtusata Quelch, 1884.

Pavona (Polyastra) venosa (Ehrenberg), Wells (1936a); Nemenzo (1955a).

Pavona (Polyastra) obtusata (Quelch); Wells (1936a); Umbgrove (1940); Nemenzo (1955a); Stephenson & Wells (1955); Scheer (1964a).

Wells (1936a) included three species, *P. venosa*, *P. planulata* and *P. obtusata* in the subgenus *Polyastra* which is primarily distinguished from *Pavona (Pavona)* by its 'strongly elevated fused walls', by its massive growth form and by the collines, which in *Pavona (Pavona)* 'usually do not encircle groups of calices, but extend between several rows of corallites perpendicular with the growing margin of the corallum, and have rounded margins'. Of these species, *P. planulata* has subsequently been placed in the genus *Gardineroseris* along with its junior synonym, *Agaricia ponderosa* Gardiner (see p. 68). The remaining two nominal species (figured by Wells, 1936a) are synonymised as variants of the one, as described below.

Although *P. venosa* is distinguished from most other *Pavona* by the characters noted above, it remains very close to some forms of *P. varians* (as noted by Wells), and for this reason, and also because there is only one species involved, it is not here distinguished as a separate subgenus. In support of this view it may be noted that both Vaughan (1918) and Crossland (1952) confused these species (Plate 57, Figs. 1, 1a and Plate XIII, Figs. 1, 2 respectively) as already pointed out by Stephenson & Wells (1955). Van der Horst (1922a) included *P. calcifera* as a synonym of *P. varians*.

Figs. 55-57 *Pavona venosa*

Fig. 55 From Fantome Island, Palm Islands, collecting station 34 (× 2.5).
Fig. 56 From Low Isles (× 2.5).
Fig. 57 From Hope Island (× 4.0).

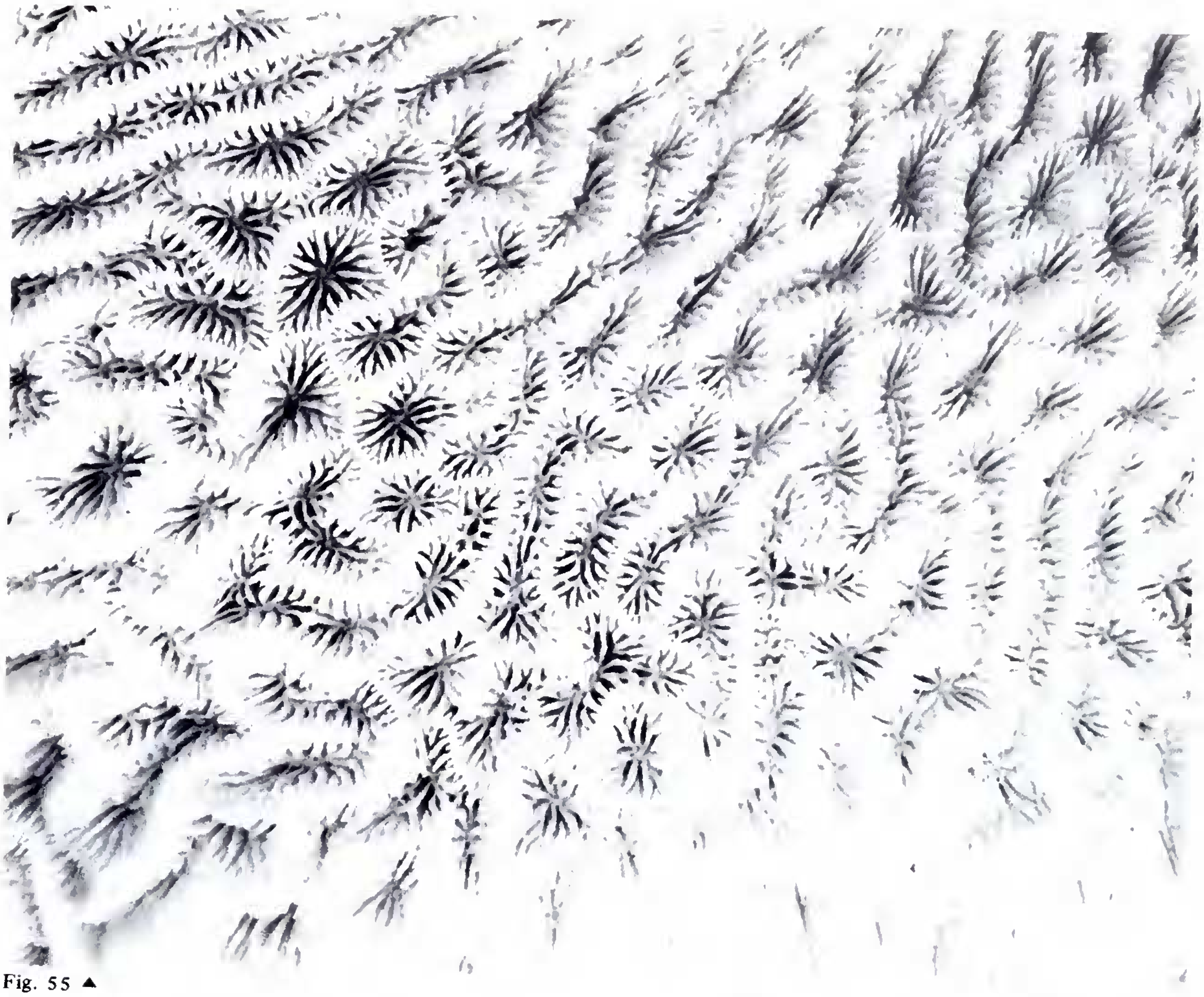
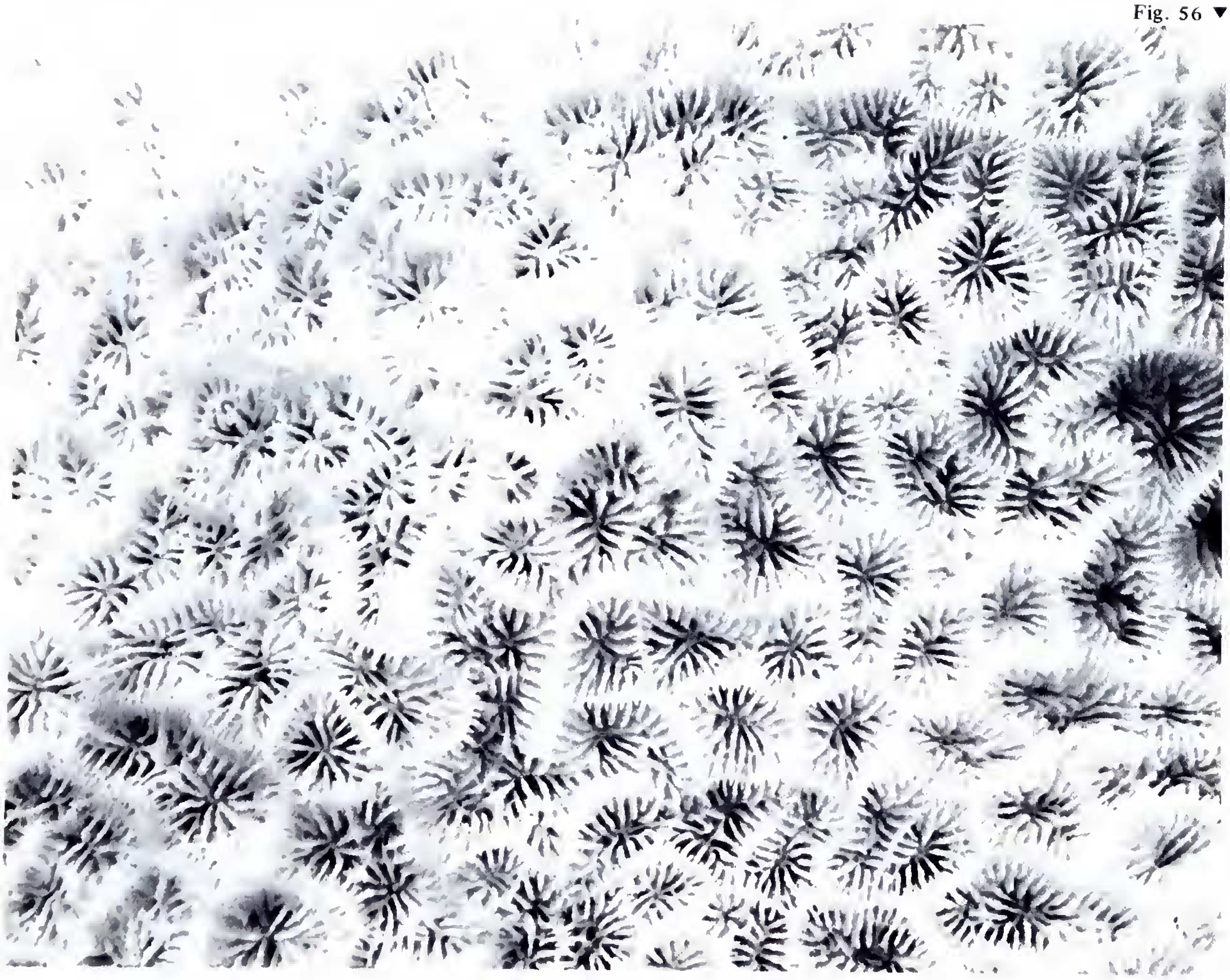


Fig. 55 ▲

Fig. 56 ▼



Crossland himself noted the close similarity between Quelch's *Tichoseris obtusata* and Gardiner's *P. calcifera.* The type specimen of the latter is identical with Great Barrier Reef *P. venosa.*

Material studied

Darnley Island, Yorke Island, Dungeness Island (5 specimens), **Murray Islands** (2 specimens), barrier reef E of **Murray Islands, Ashmore Reef, Lizard Island, Eyrie Reef** (3 specimens), **Hope Island** (5 specimens), **Low Isles** (2 specimens), **Palm Islands** (4 specimens), **Heron Island.**

These localities include collecting stations 11, 12, 13, 19, 27, 29, 34, 35, 43, 45, 107, 110, 122.

Previous records from Eastern Australia

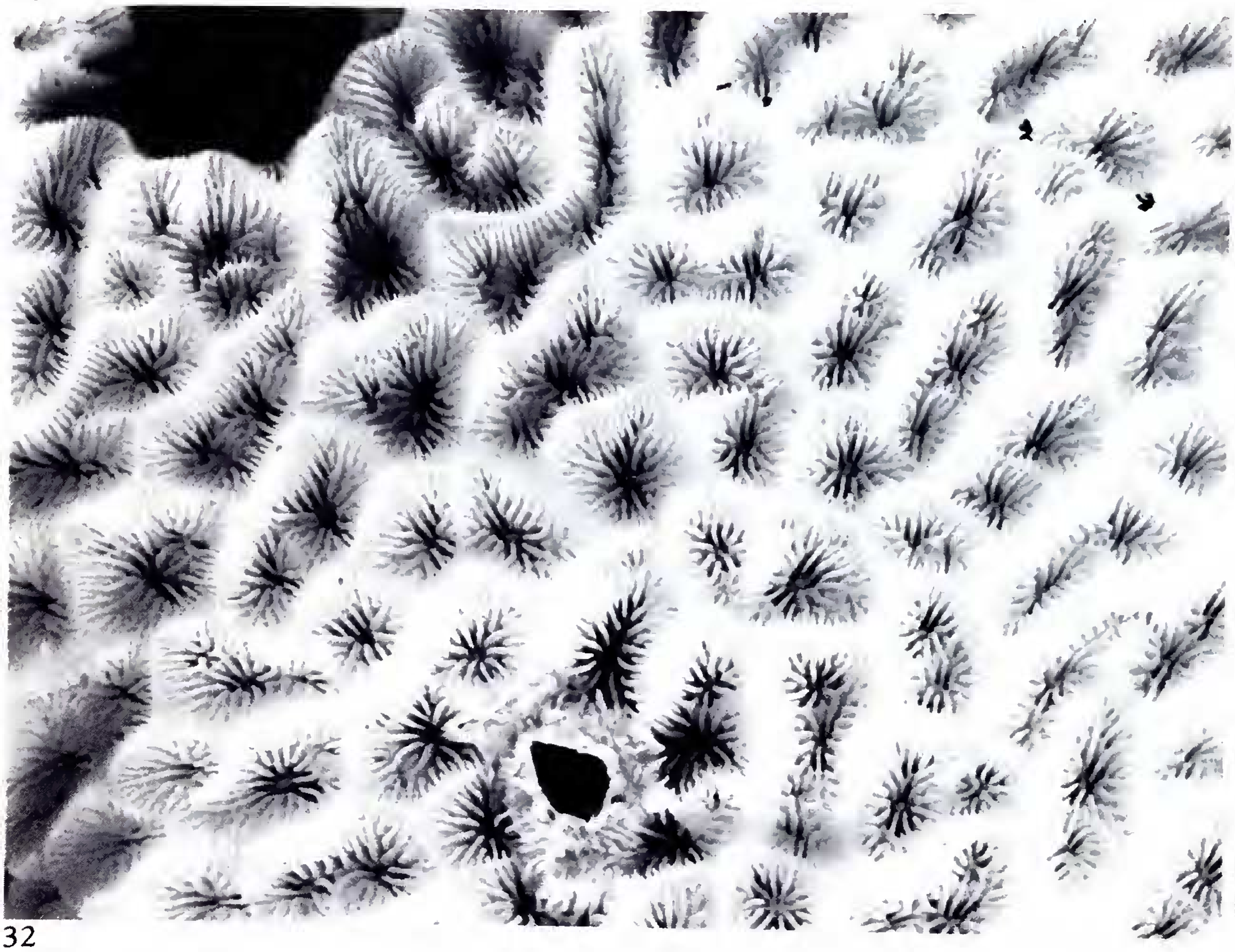
Murray Islands (as *P. varians, pars*) Vaughan (1918); **Low Isles** (as *P. varians pars.*) Crossland (1952), (as *P. (Polyastra) obtusata*) Stephenson & Wells (1955);

Murray Islands (as *P. varians, pars*) Vaughan (1918); **Low Isles** (as *P. varians, pars*) Crossland (1952), (as *P. (Polyastra) obtusata*) Stephenson & Wells (1955);

Characters

Colonies are massive, hemispherical to clavate. Corallites are discrete or arranged in valleys, either with a small number of irregularly grouped centres, or with many centres arranged at the bottom of straight to sinuous shallow depressions. This wide variation is commonly found on a single specimen, corallites and/or valleys varying from 0.5 to 2.5 mm diameter. Centres arranged in valleys are separated by 1 to several trabecular linkages with little development of a theca. Thin, high thecae are sometimes developed. Three orders of septa can be distinguished in most coralla. The first order consists of 5-12 high septa extending almost to the calice centre. Second and third order septa occur in regular sequence,

Fig. 57 ▼



the latter usually being developed only near the thecal rim. All septa are thin and regularly spaced, with granulated sides and smooth to slightly dentate margins. There is little or no development of a columella.

Affinities

As previously noted, this species may sometimes resemble *P. varians* (see pp. 28 and 30)(Figs. 735, 736).

Distribution

The relatively few records of this species indicate a wide distribution from the Red Sea in the west to the Celebes, Indonesia and several Pacific Islands, eastward to the Marshall Islands.

Pavona maldivensis (Gardiner, 1905)

Synonymy

Siderastrea maldivensis Gardiner, 1905 *(pars).*

Pavona maldivensis (Gardiner), Matthai (1948a).

Pavona (Pseudocolumnastrea) pollicata Wells, 1954; Ma (1959).

These two specific names apply to the two basic growth forms of this one species. The holotype of *P. maldivensis* (Fig. 63) is a small encrusting plate, that of *P. pollicata* is mostly columnar. The name *P. maldivensis* has been used for many species, but not correctly except by Matthai, since Gardiner's original description. It should be noted that only Pl. LXXXIX, Fig. 3 is this species, Figs. 1 and 2 are of *P. clavus.*

Fig. 58 Holotype of *Pavona venosa* (× 5).

Material studied

Bramble Cay (2 specimens), **Ashmore Reef** (4 specimens), **Yonge Reef** (2 specimens), **Palm Islands** (8 specimens), **Parker Reef** (3 specimens), **Bushy Island-Redbill Reef, Pompey Complex** (5 specimens), **Swain Reefs** (4 specimens), **Heron Island, Wistari Reef** (3 specimens), **Lord Howe Island** (4 specimens).

These localities include collecting stations 3, 9, 33, 35, 37, 56, 67, 69, 72, 75, 76, 77, 80, 81, 105, 106, 117, 118, 128, 143.

Previous records from Eastern Australia

Lord Howe Island, Veron & Done (1979).

Characters

Two basic growth forms occur, sometimes within the one colony. The first is primarily encrusting with thin, free, laminar margins, commonly up to 30 cm across (Fig. 61). The second is digitate with vertical or diverging clavate branches with irregular diameters averaging 2 cm. Sub-branches of similar diameter form at irregular intervals. Such colonies are seldom more than 20 cm high, although very large colonies usually combining both growth forms may be found in protected environments (Fig. 62).

Corallites are mostly circular, 2-4 mm diameter. They are radially symmetrical or inclined towards the margins of laminar plates. They may be compact or separated by average distances up to 6 mm. Thecae are distinct, usually protruding up to 2 mm except on branch ends. Septo-costae are typically pavonid, either equal or alternating, closely compacted, 15-25 in number. Where distinguished, first order septo-costae project slightly further into the calices and tend to be more continuous with adjacent corallites than those of the second order. All septo-costae have densely granulated sides and smooth, sometimes laterally crenellated, margins. The inner margins plunge steeply within the calices and are usually vertical at the level of the columella. Septo-costae are usually perpendicular to the free margins of laminar coralla, but have no fixed direction in digitate forms. The columella is solid, either peg-like or elongate, and is composed of a few fused trabeculae. Approximately 10 septa reach the columella. Synapticular processes are usually clearly seen on branch ends where they contribute much of the skeleton of the thecae. The undersurface of laminar plates is smooth or very finely striate.

Budding is primarily extratentacular. Occasionally, costae with free margins give rise to thamnasteroid-like protrusions, sometimes accompanied by alveoli, which frequently appear to be primordial calices.

Colonies are usually dark coloured, either brown or green; polyp tentacles are usually pale and distinctive (Fig. 737).

Affinities

The subgenus *Pseudocolumnastrea* Yabe & Sugiyama, 1933 formerly included *P. yamanarii* Yabe & Sugiyama and *maldivensis* Gardiner (1905) which are primarily characterised by circular, plocoid or sub-plocoid corallites. The holotype of *P.*

Figs. 59-62 *Pavona maldivensis*, Figs. 59-61 (× 0.5).

Fig. 59 From the Swain Reefs, collecting station 67, showing extreme development of a digitate growth form.

Fig. 60 From Lord Howe Island, collecting station 143, showing a partly digitate, partly explanate growth form.

Fig. 61 From Lord Howe Island, collecting station 147, showing extreme development of an explanate growth form.

Fig. 62 From Ashmore Reef, collecting station 206, showing development of digitate branches on fine, encrusting laminae, characteristic of coralla from caves or under overhangs (× 1.0).

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yamanarii, a fossil, is the top of a laterally compressed, sub-massive column distinguished from *P. maldivensis* by the presence of a styliform columella and paliform lobes; otherwise they are similar.

The name *P. maldivensis* has been erroneously used by all authors except Matthai (1948a). Vaughan (1918) and van der Horst (1922a) both considered *P. maldivensis* to be synonymous with, or close to *P. clavus.* Wells (1954) considered *P. maldivensis* to be in the subgenus *Pseudocolumnastrea* and noted resemblances between this species and his new *P. pollicata.*

Distribution

This little-known species is widely distributed throughout the Indo-Pacific, from Madagascar in the west to the Marshall Islands in the east.

Fig. 63 Holotype of *Pavona maldivensis* (× 2.5).

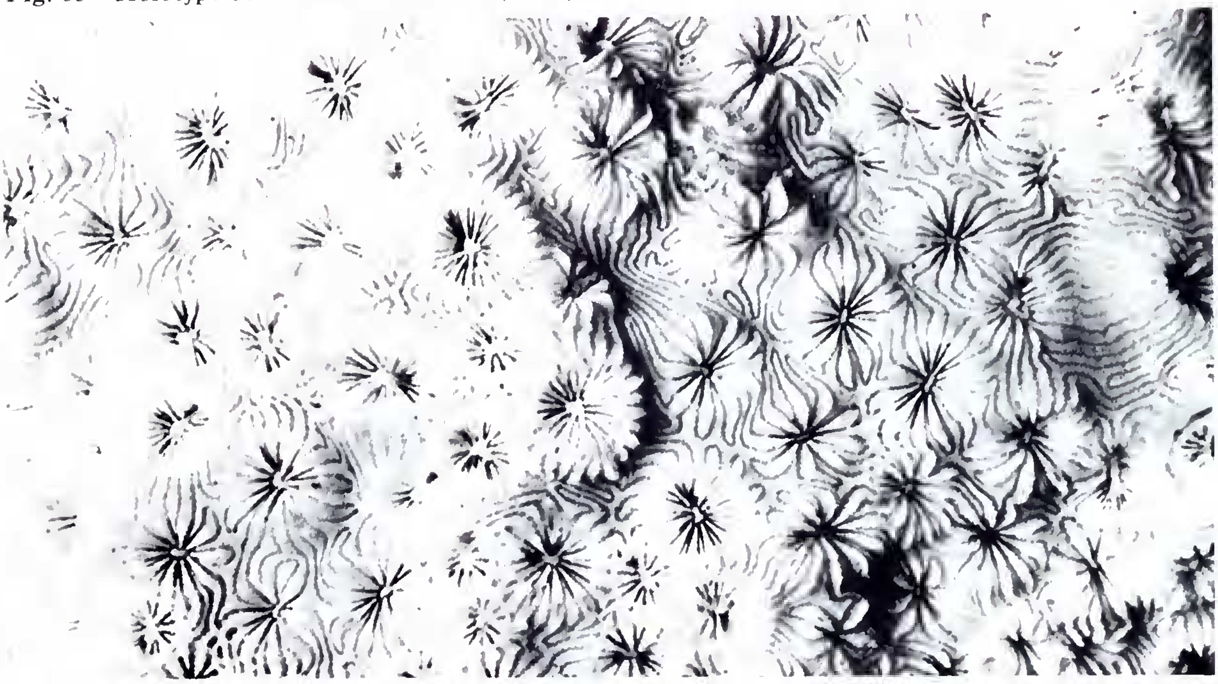


Fig. 64 *Pavona maldivensis* from the Swain Reefs.

Generic synonymy

Leptoseris Edwards & Haime, 1849c.

Haloseris Edwards & Haime, 1849c.

Helioseris Edwards & Haime, 1849c *(pars)*.

Domoseris Quelch, 1886.

Cylloseris Quelch, 1886.

Folioseris Rehberg, 1892.

Agariciella Ma, 1937.

Type species *Leptoseris fragilis* Edward & Haime, 1849c.

Characters of the genus

Coralla have circumoral followed by marginal budding, forming thin, unifacial folia, crateriform to digitate. Centres are superficial, protuberant in some species; thecae are poorly developed.

Introduction

Of the 25 nominal species of true Indo-Pacific *Leptoseris*:—*Pavona papyracea* Dana (1846); *Leptoseris fragilis* Edwards & Haime (1849c) and *Haloseris crispa* Edwards & Haime (1851c); *Leptoseris striatus* Saville-Kent (1871); *Cylloseris incrustans, Domoseris porosa, D. solida* and *D. regularis* Quelch (1886); *Pavona ramosa* and *P. pretiosa* Bassett-Smith (1890); *Leptoseris gardineri* and *L. incrustans* Gardiner (1905); *L. hawaiiensis, L. scabra, L. digitata,* and *L. tubulifera* Vaughan (1907); *L. gravieri, L. gardineri* and *L. tenuis* van der Horst (1921); *L. columna* and *L. explanata* Yabe & Sugiyama (1941); *L. panamensis* Durham & Barnard (1952); *L. mycetoseroides* Wells (1956); *L. zamboi* Nemenzo (1971); *L. paschalensis* Wells (1972); *Pavona yabei* Pillai & Scheer (1976), 16 fall within the range of east Australian species. Of these, 7 nominal species are small, finely branched forms which are likely to be only variants of *L. papyracea*. The remaining 9 nominal species fall within the range of 7 true species as determined by the present study. Two of these, *L. gardineri* and *L. explanata* are well defined, having very distinctive, large, upright folia. *Leptoseris hawaiiensis* forms flat explanate plates, is uncommon, but occurs in a wide variety of biotopes.

Leptoseris scabra is one of the most common and most variable east Australian species. Its wide range of skeletal characters includes two other nominal species, *L. striatus* and *L. columna* which, despite their many differences, are here considered to be junior synonyms of *L. scabra*. The remaining species, *L. mycetoseroides, L. tenuis* and *L. yabei* have well defined characters showing close affinities to *Gardineroseris* and *Pavona* species.

The other nominal species of *Leptoseris* are very clearly not included in the present collections. Of the four species of Quelch, all from Tahiti, *Domoseris (= Leptoseris) solida* and *D. porosa* are virtually identical and *D. regularis* appears to be an immature colony of the same species. His *Cylloseris (= Leptoseris) incrustans* is a separate, very distinctive but little known, mostly encrusting species of *Leptoseris*. *Leptoseris paschalensis* Wells is very close to, if not the same as, *L. solida*. *Leptoseris tubulifera* Vaughan from Hawaii has been widely confused with *L. scabra* because both species may have tubular branches. However, the former, having very fine branches with many distinctive characters, is very different from eastern Australian *L. scabra*. *Leptoseris incrustans* Gardiner (not Quelch) is close to *L. hawaiiensis* but is a distinct species not found in eastern Australia. *Leptoseris gravieri* is, in the present study, considered to be a probable junior synonym of *Pavona explanulata* (see p. 17).

Leptoseris papyracea (Dana, 1846)

Synonymy (partly after Wells, 1952).

Pavona papyracea Dana, 1846; Bassett-Smith (1890).

Haloseris crispa Edwards & Haime, 1851c.

Pavonia ramosa Bassett-Smith, 1890.

Pavonia pretiosa Bassett-Smith, 1890.

Leptoseris papyracea (Dana); Verrill (1864); van der Horst (1921, 1922a); Faustino (1927); Matthai (1948c); Wells (1954).

Leptoseris digitata Vaughan (1907); Matthai, 1948c.

Leptoseris panamensis Durham & Barnard, 1952.

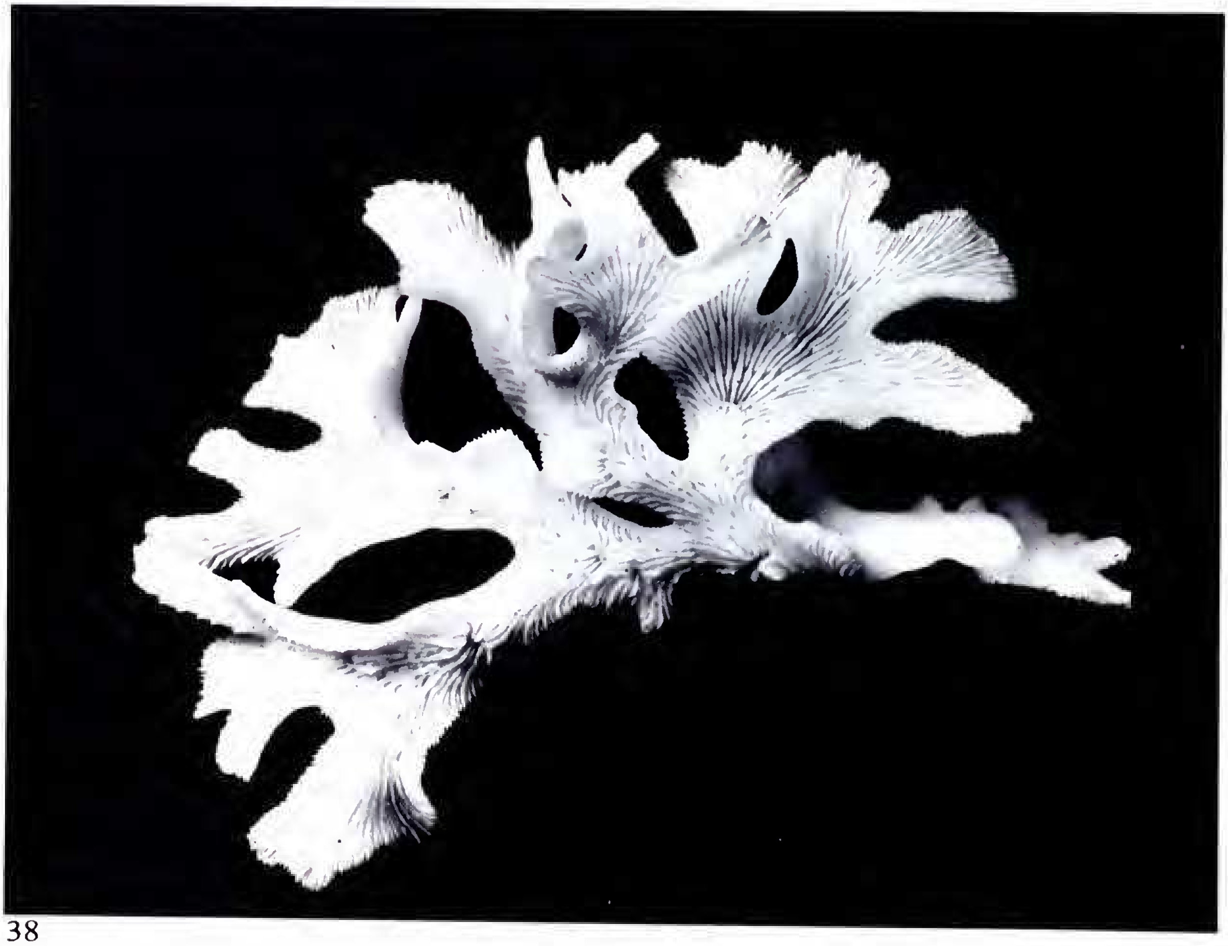
Leptoseris zamboi Nemenzo, 1971.

The type specimens of *L. digitata* and *L. pretiosa* are almost identical, as are *L. crispa* and *L. ramosa*. The latter two species differ from the former in having slightly more prominent costae, less prominent columellae, and shorter branches. However, all four species are close to *L. papyracea*.

Leptoseris zamboi Nemenzo was described from a single, relatively large colony having essentially the same growth form as the other nominal species included in *L. papyracea*. Otherwise it is separated only by the virtual absence of columellae (prominent in *L. digitata*), a variable character in the present series. There is almost no difference between *L. zamboi* and *L. crispa*, also from the Philippines.

Figs. 65, 66 *Leptoseris papyracea* from the horizontal sea floor east of Magnetic Island (× 2.5).

Fig. 65 ▼



Leptoseris panamensis from western Panama is the same or a similar species. The small fragments examined by the authors indicate a similar size and growth form except that branches are thicker. The few fine skeletal details observable are consistent with those of *L. papyracea*.

Material studied

Dredged west of **Bowl Reef**, 55 m; E of **Magnetic Island**, 30 m.

Previous records from Eastern Australia

Not previously recorded.

Characters

The present small series of specimens consists of irregularly contorted fronds up to 2 cm across, but mostly much smaller (average 5 mm) and <3 mm thick (Figs. 65, 66). Corallites are axial on narrow branches and irregularly distributed on broader ones. They are superficial, with relatively well defined thecae, and are usually slightly inclined towards the branch ends. Calices are elliptical <2.5 mm diameter. Two orders of septo-costae can usually be distinguished running predominantly lengthwise. Second order septo-costae gradually grade into first order as branch diameters increase. All septo-costae are very fine; they are only slightly granulated and are relatively widely spaced. Septa have steep inner margins; 12-20 reach the columellae. The structure of the columella is variable; in some specimens they are little developed, in others they are composed of a high mound of twisted trabeculae. The undersurface of branches is smooth or finely costate.

Fig. 66 ▼

Affinities

This species resembles only *P. gardineri* with which it was originally confused (see below). It is much finer than that species with very much smaller branches and smaller, more superficial corallites.

Distribution

The distribution of *L. papyracea* cannot be fully determined without further study of some of the questionable junior synonyms noted above. It extends to the western Indian Ocean (Madagascar and Amirante Islands) and eastward to Hawaii. If *L. panamensis* is the same species, it ranges to the far eastern Pacific Ocean.

Leptoseris gardineri van der Horst, 1921

Synonymy

Pavona papyracea Dana; *sensu* Gardiner (1905).

Leptoseris gardineri van der Horst, 1921; Hoffmeister (1925); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Yabe & Sugiyama (1941); Wells (1954); Ma (1959); Scheer (1972).

Van der Horst (1921) noted that both Rehberg (1892) and Gardiner (1905) misidentified this species as *P. papyracea*, and renamed it.

Material collected

Palm Islands (10 specimens), **Whitsunday Islands** (2 specimens), **Pompey Complex** (4 specimens).

These localities include collecting stations 42, 43, 59, 72, 90, 91, 96, 97.

Previous records from Eastern Australia

Latitude of **Cairns** to **Whitsunday Islands**, Wells (1955a).

Characters

Extensive outcrops of this species are frequently found around high islands where individual colonies may exceed 6 m diameter. Only the upper, approximately 20 cm of these colonies are alive and consist of delicate, bifurcating branches with lobed, flat or recurved margins (Figs. 67, 68). Branches are usually <2 cm across and contain 1-3 corallites abreast. Calices are slit-like or elliptical with a maximum dimension of <4 mm (Fig. 69). The thecal rim is usually distinct. Septo-costae are arranged alternately, frequently second order costae become first order when a new lateral pair of second order costae develop. All septo-costae are lightly granulated with those of the first order being thicker, more exsert and more granulated. They primarily radiate from the calice centres to reach the margins or to extend along the branch to the next calice (Fig. 70). They plunge vertically within the calices, which are deep except at the periphery, 8-12 of the first order reaching the columellae. The columellae are situated deep within the calices and usually consist of a fused mass of trabeculae with similar shapes as the calices. The backs of branches are smooth with fine costal striations just visible. Even vertical branches are never bifacial.

Living colonies are usually cream, pale brown or yellow.

Figs. 67-70 *Leptoseris gardineri.*

Figs. 67, 69 From the Pompey Complex, collecting station 72 (× 0.5 and 0.8 respectively).
Figs. 68, 70 From Orpheus Island, Palm Islands, collecting station 91 (× 2.0 and 4.5 respectively).

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Affinities

This species has not been found in the same biotope as *L. papyracea* to enable *in situ* comparison. The latter has much finer branches with smaller, usually axial, corallites. There is a closer resemblance to *Leptoseris explanata* which occupies similar habitats and which may have a similar growth form. *Leptoseris explanata* has wider branches with larger, more prominent corallites, with more septa and markedly unequal septo-costae.

Distribution

Known from the Maldive Islands and the central Indo-Pacific east to Samoa and Fiji.

Leptoseris explanata Yabe & Sugiyama, 1941

Synonymy

Leptoseris explanata Yabe & Sugiyama, 1941.

Leptoseris hawaiiensis Vaughan; *sensu* Yabe & Sugiyama (1941).

Leptoseris scabra Vaughan; *sensu* Matthai (1948a).

The type specimen (Figs. 80, 81) is a small flat plate most closely resembling deep-water specimens of the present series (Fig. 79). It differs substantially from the rest of the series in having smaller corallites and less prominent septo-costae.

Material studied

Black Rocks, Yorke Island, dredged 8 km NE **Murray Islands, Murray Islands, Torres Strait, Palm Islands** (16 specimens), dredged W of **Bowl Reef, Whitsunday Islands** (2 specimens).

These localities include collecting stations 29, 34, 42, 43, 59, 90, 94, 97, 107, 125, 127.

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies have a wide variety of shapes (Fig. 738) including flat laminar plates, vase shapes and flat, mostly horizontal bifurcating, diverging branches. The latter are broad with corallites distributed irregularly. Colony margins are thin and delicate; older parts of most colonies are over 1 cm thick and the skeleton is dense and heavy (cf. *P. gardineri*). Calices are elongate to circular, <6 mm maximum dimension and are usually inclined towards the margins. Septo-costae are very unequal; those of the first order are thicker, markedly more exsert and more granulated. Up to 30 first order septa reach the columella. In one specimen from 55 m depth (Fig. 79), three orders of costae are clearly visible. All septo-costae regularly radiate from the calices then run perpendicular to the margin. Frequently second order septo-costae become first order when lateral pairs of secondary costae branch. Very small alveoli can usually be seen at the insertion of new costae. Carinae are not developed. Corallites are filled with a dense, conspicuous, spongy columella of fused trabeculae. The thecae,

Figs. 71-75 *Leptoseris explanata* (× 0.5).

Fig. 71	From Juno Bay, Fantome Island, Palm Islands, collecting station 11.
Fig. 72	From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.
Figs. 73, 74	From Pelorus Island, Palm Islands, collecting station 90.
Fig. 75	From W of Bowl Reef.

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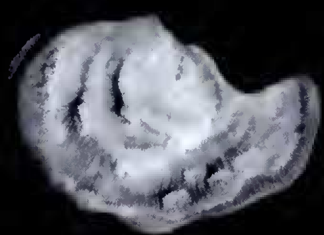

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particularly their inner margins, are relatively well defined. They are initially synapticular then become secondarily thickened with dissepiments. The undersurface of coralla is smooth or very finely striated. Living colonies are pale brown.

Affinities

Leptoseris explanata is perhaps closest to *L. gardineri* (see p. 42). It may also resemble some colonies of *L. scabra* and, to a lesser extent, *L. tenuis*, both of which are readily distinguished by their lack of prominent, alternating costae.

Distribution

Previous records are from Palau (Yabe & Sugiyama, 1941) and the Red Sea (Matthai, 1948a).

Figs. 76-79 *Leptoseris explanata* (× 5.0).

Fig. 76 From Nara Inlet, Hook Island, same corallum as Fig. 72.
Figs. 77, 78 From Pelorus Island, same coralla as Figs. 73, 74 respectively.
Fig. 79 From Bowl Reef, same corallum as Fig. 75.

Fig. 76 ▼

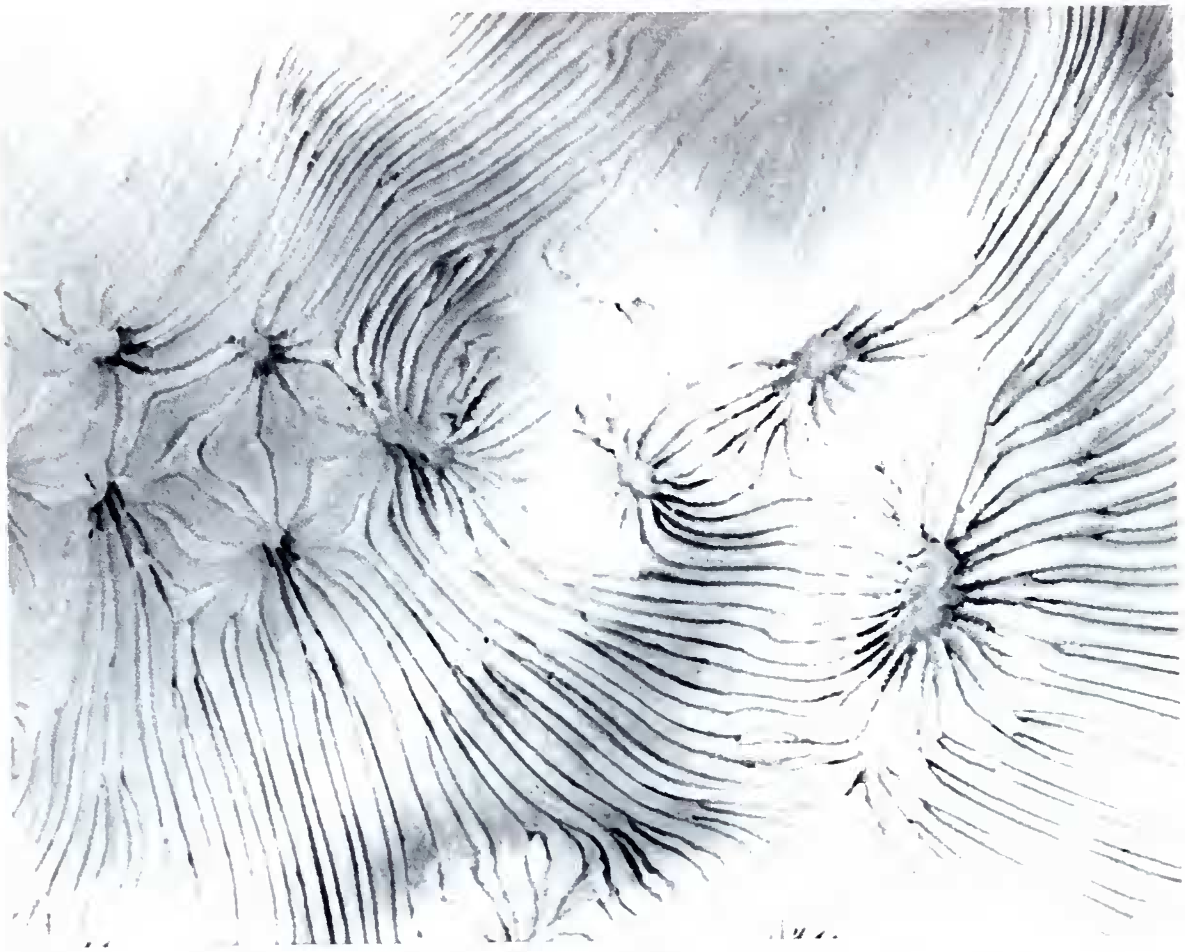
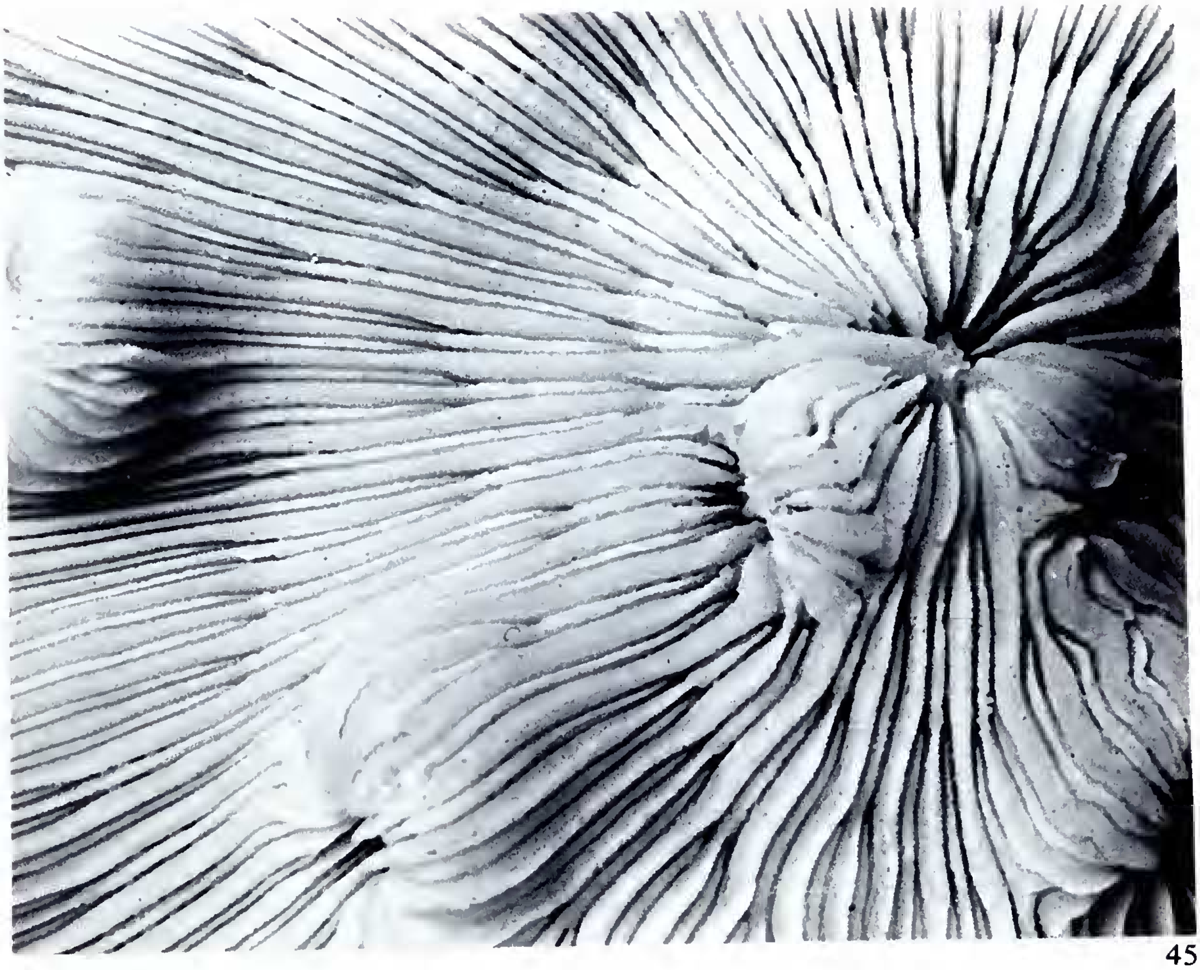


Fig. 77 ▲

Fig. 78 ▼



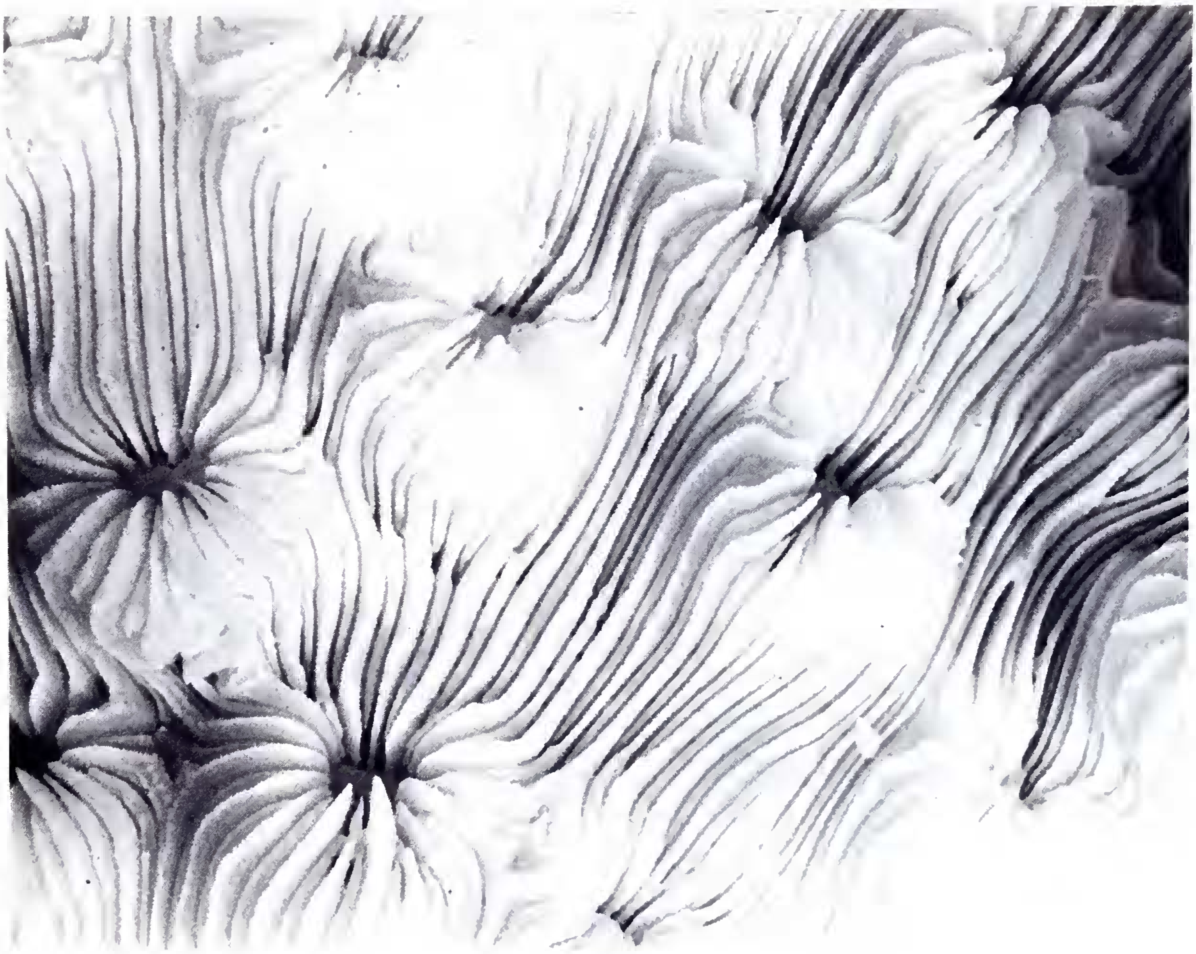


Fig. 79 ▲

Figs. 80, 81 Holotype of *Leptoseris explanata* (× 0.5 and 5.0 respectively).

Fig. 80 ▼

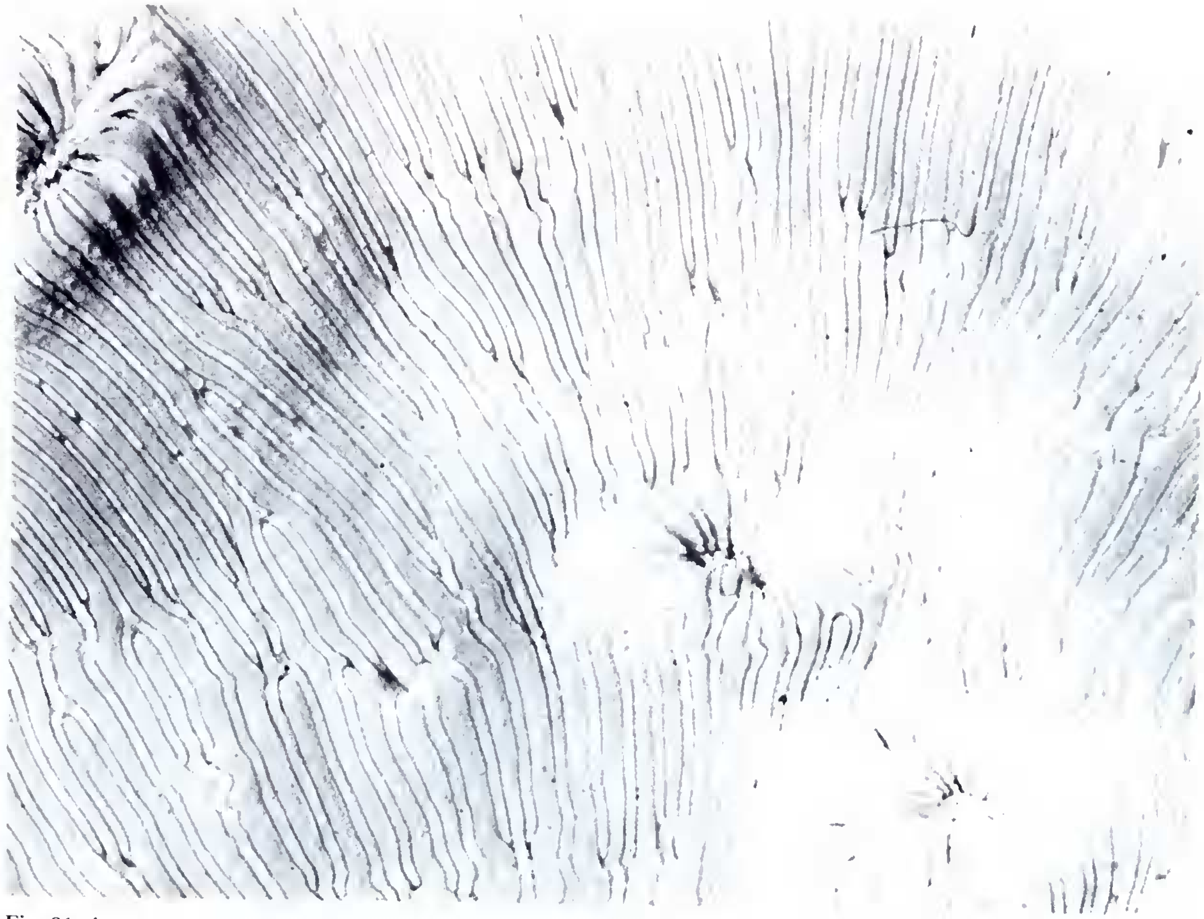


Fig. 81 ▲

Fig. 82 *Leptoseris explanata* at Eclipse Island, Palm Islands, collecting station 59.

Fig. 82 ▼

Leptoseris scabra Vaughan, 1907

Synonymy

Leptoseris striatus Saville-Kent, 1871.

Leptoseris scabra Vaughan, 1907a; Hoffmeister (1925); Wells (1954); Ma (1959); Chevalier (1968); *non* Matthai (1948a).

Leptoseris columna Yabe & Sugiyama, 1941; Ma (1959).

Leptoseris tubulifera Vaughan; *sensu* van der Horst (1922a).

The holotype of *L. striatus*, from Borneo, is a young colony 4.6 cm long having only three corallites. Nevertheless it clearly belongs to the species described below. Likewise, co-type USNM 20886 of *L. scabra* from Hawaii and the holotype of *L. columna* from Palau, clearly fall within the range of variation of this species. The name *L. striatus* is dropped by the present authors, *nomen oblitum*, because it has not been used since Saville-Kent's original description. However, it should be noted that there are differences between most of the type series of *L. scabra* and most of the present series, the type series having come from an isolated locality at an extreme of the species' geographic range.

Material studied

Bramble Cay (4 specimens), **Anchor Cay, Yorke Island** (3 specimens), barrier reef 8km NE of **Murray Islands, Murray Islands** (8 specimens), **Ashmore Reef** (4 specimens), **Great Detached Reef** (2 specimens), **Tijou Reef** (2 specimens), **Jewell Reef** (5 specimens), **Yonge Reef** (6 specimens), **Lizard Island** (3 specimens), **Ribbon Reef, Low Isles, Palm Islands** (41 specimens), **Whitsunday Islands** (8 specimens), **Swain Reefs** (3 specimens), **Heron Island, Wistari Reef, Lord Howe Island** (3 specimens).

These localities include collecting stations 3, 5, 8, 9, 27, 29, 33, 34, 35, 38, 42, 43, 45, 55, 56, 58, 59, 65, 78, 81, 90, 91, 92, 93, 97, 98, 106, 107, 117, 125, 126, 128, 135, 147.

Previous records from Eastern Australia

Lord Howe Island, Veron & Done (1979).

Characters

A general lack of conservative skeletal characters makes this species particularly difficult to separate from other closely allied species. All coralla are initially encrusting and budding is circumoral. Colonies develop free laminar margins which are extended, either as irregular plates, or become contorted, thin walled, hollow columns and open-ended tubes. These columns and tubes frequently anastomose. Sometimes they expand into a new laminar plate which supports another layer of contorted growth, giving such coralla an extremely irregular appearance (Fig. 87).

The distribution of corallites is no less irregular. Most encrusting coralla have centres approximately 6-10 mm apart irrespective of position on the corallum. Those with extended thin laminar margins have decreasing numbers of centres towards the margins, some with no centres closer than 2.5 cm from the margins. Some corallites may be indistinct in highly contorted coralla where they consist of little more than centres of radiating septo-costae accompanied by carina-like folds.

Figs. 83-87 *Leptoseris scabra* (× 0.5).

Fig. 83 From Barber Island, Palm Islands, collecting station 93, showing a submassive growth form.
Fig. 84 From Curacao Island, Palm Islands, collecting station 56, showing an explanate growth form.
Fig. 85 From Dido Rock, Palm Islands, collecting station 58.
Fig. 86 From Orpheus Island, Palm Islands, collecting station 91, showing the development of open-ended tubes.
Fig. 87 From Yonge Reef, collecting station 3, showing an extreme development of convoluted tubes.

83

84

85

86

87

Septo-costae may be sub-equal to very unequal, in two alternating orders. In the latter case, second order costae may change abruptly into first order at the insertion of a new, adjacent, pair of second order costae. This change may occur in rows involving many costae, the rows being concentric with the parent corallite. Costae of the first order are usually markedly thicker and slightly more exsert with first order septa frequently being markedly exsert over the thecae. First order septo-costae, particularly those toward the centre of laminar or encrusting coralla, have rough margins composed of irregular pinnacles or lobes which are heavily granulated. In such cases they are up to 1 mm thick and are usually markedly crenellated. Six to twenty first order septa reach the columella. Second order septo-costae are usually more regular, less pinnacled and less granulated. Their margins may be entire, very finely keeled or tri-ridged. Columellae are deep seated, small, pinnacle-like, or elongate. Thecae are usually thick, especially on the inner margin. The undersurface is smooth or finely costate.

Living colonies are usually dull grey, brown or green. Sometimes the margins have a well defined white border (Fig. 739).

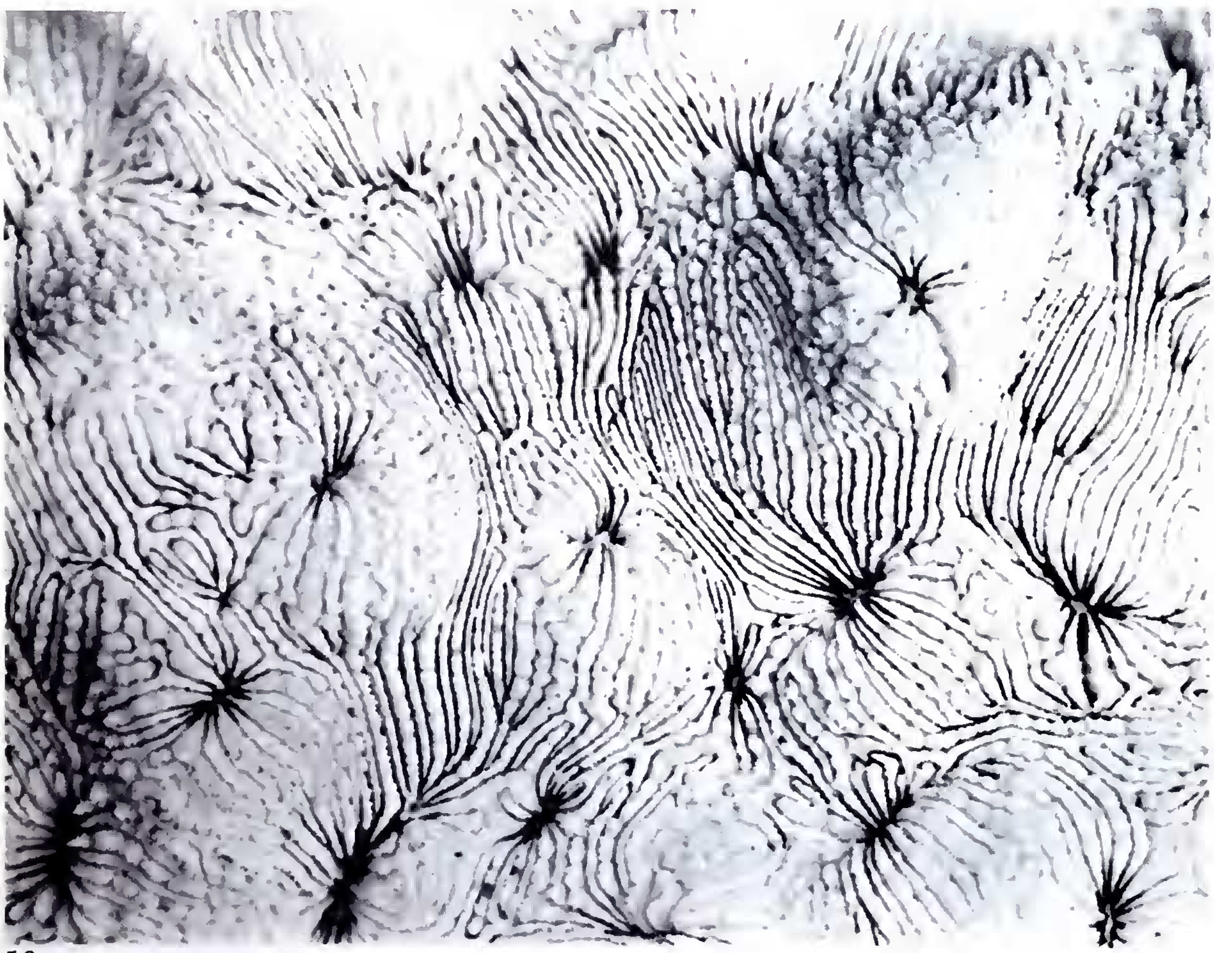
Affinities

Some plate-like coralla of the present series, as well as the holotype of *L. columna*, resemble Quelch's types of *L. solida* and *L. porosa* as well as *L. paschalensis* Wells.

Figs. 88-91 *Leptoseris scabra*, Figs. 88, 89 (× 5.0) Figs. 90, 91 (× 2.0).

Fig. 88 From Barber Island, same corallum as Fig. 83.
Fig. 89 From Dido Rock, same corallum as Fig. 85.
Fig. 90 From Orpheus Island, same corallum as Fig. 86.

Fig. 88 ▼



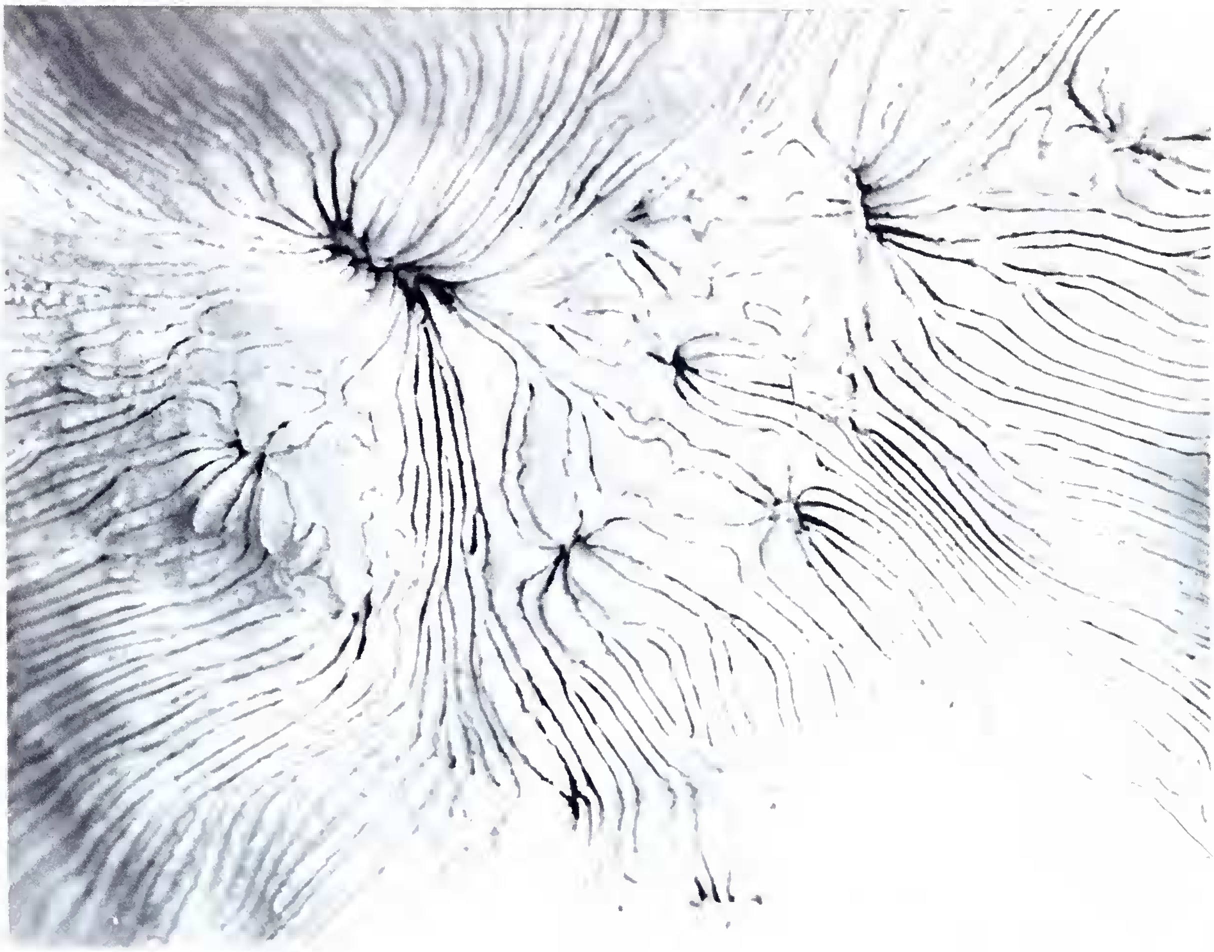


Fig. 89 ▲

Fig. 90 ▼

Fig. 91 From Yonge Reef, same corallum as Fig. 87.

All have inclined corallites with highly contorted, sometimes crenellated, costae. They are primarily distinguished by having larger corallities which usually vary greatly on different parts of the same corallum.

Among Great Barrier Reef species, plate-like specimens of *L. scabra* resemble *L. hawaiiensis* which may also have highly crenellated costae. The latter species has smaller, less protuberant corallities, with deep round calices and usually very even costae.

Distribution

Widespread from the western Indian Ocean to the western Pacific, extending east to Hawaii.

Leptoseris hawaiiensis Vaughan, 1907

Synonymy

Leptoseris hawaiiensis Vaughan, 1907a; van der Horst (1921, 1922a); Matthai (1924, 1948a, 1948c); Wells (1954); Ma (1959); *non* Yabe & Sugiyama (1941).

Only three of Vaughan's 15 co-types have been studied by the present authors. These differ substantially from each other and only USNM 20843 (Figs. 97, 98) conclusively fits into the present series from the Great Barrier Reef. Specimens from Lord Howe Island are generally closer to the type series. Both series are from the species geographic extremes.

Fig. 92 *Leptoseris hawaiiensis* from Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98 (× 0.5).

Material studied

Bramble Cay (3 specimens), **Black Rocks, Anchor Cay, Big Mary Reef, Yorke Island, Dungeness Island, Murray Islands** (3 specimens), **Ashmore Reef** (5 specimens), **Yonge Reef, Ribbon Reef, Palm Islands** (6 specimens), **Whitsunday Islands, Bushy Island-Redbill Reef, Swain Reefs** (3 specimens), **Lord Howe Island** (4 specimens).

These localities include collecting stations 3, 27, 28, 58, 63, 78, 90, 98, 106, 107, 112, 123, 126, 127, 128, 129, 131, 143.

Previous records from Eastern Australia

Lord Howe Island, Veron & Done (1979).

Characters

Coralla are encrusting, laminar or funnel-shaped. Frequently a central corallite is visible with subsequent corallites distributed irregularly, or in short, approximately concentric, rows. Central corallites may be radially symmetrical but most other corallites are inclined towards the corallum margins. Calices are circular or (more commonly) elliptical, usually <3 mm diameter. Septo-costae are equal or very slightly alternate. They vary in thickness (<1 mm), but are evenly spaced and equally exsert.

Figs. 93-96 *Leptoseris hawaiiensis*, Figs. 93, 94 (× 2.5), Figs. 95, 96 (× 5.0).

Fig. 93 From Butterfly Bay, Hook Island, same corallum as Fig. 92.
Figs. 94, 95 From the Swain Reefs, collecting station 78.
Fig. 96 From Pelorus Island, Palm Islands, collecting station 90.

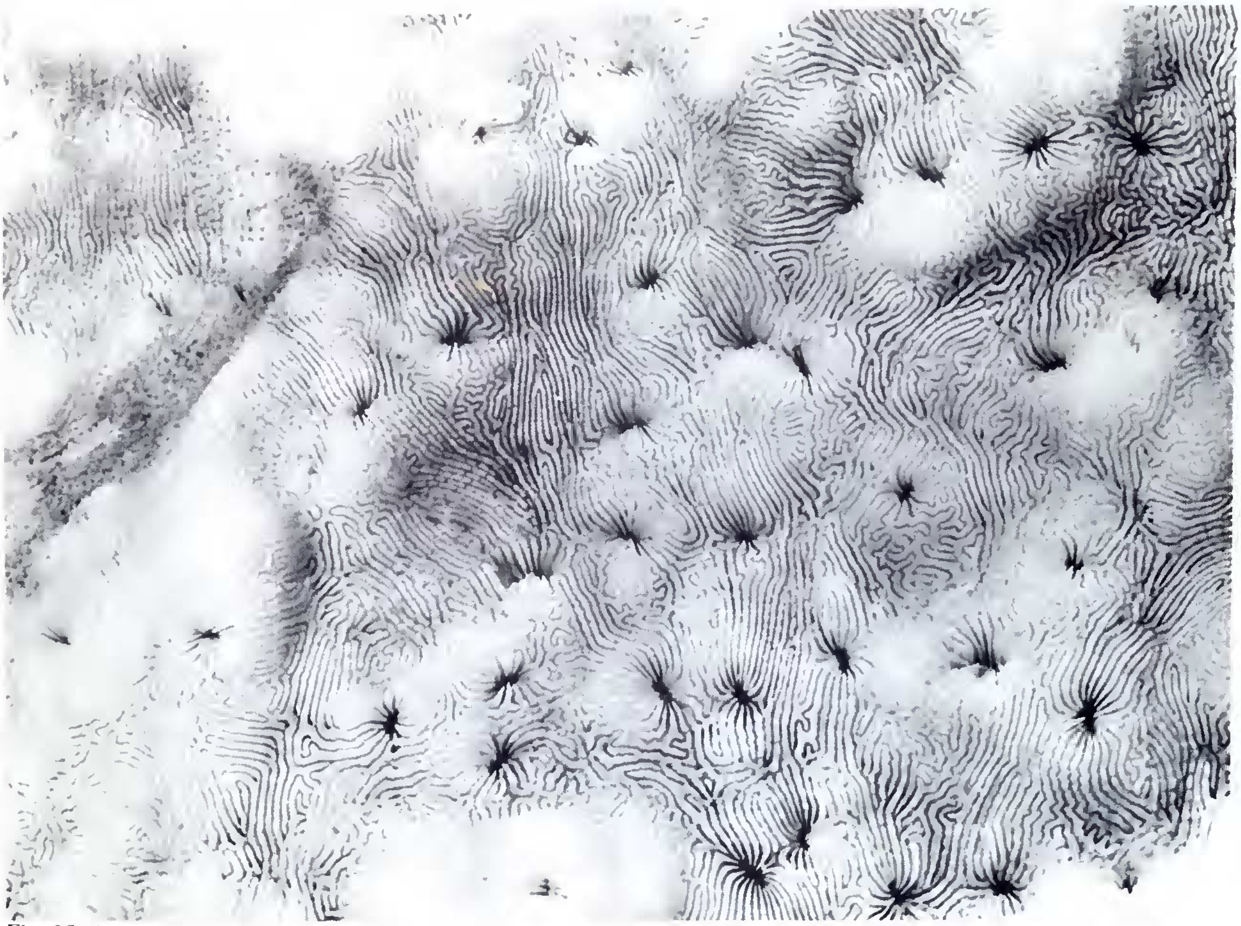


Fig. 93 ▲

Fig. 94 ▼

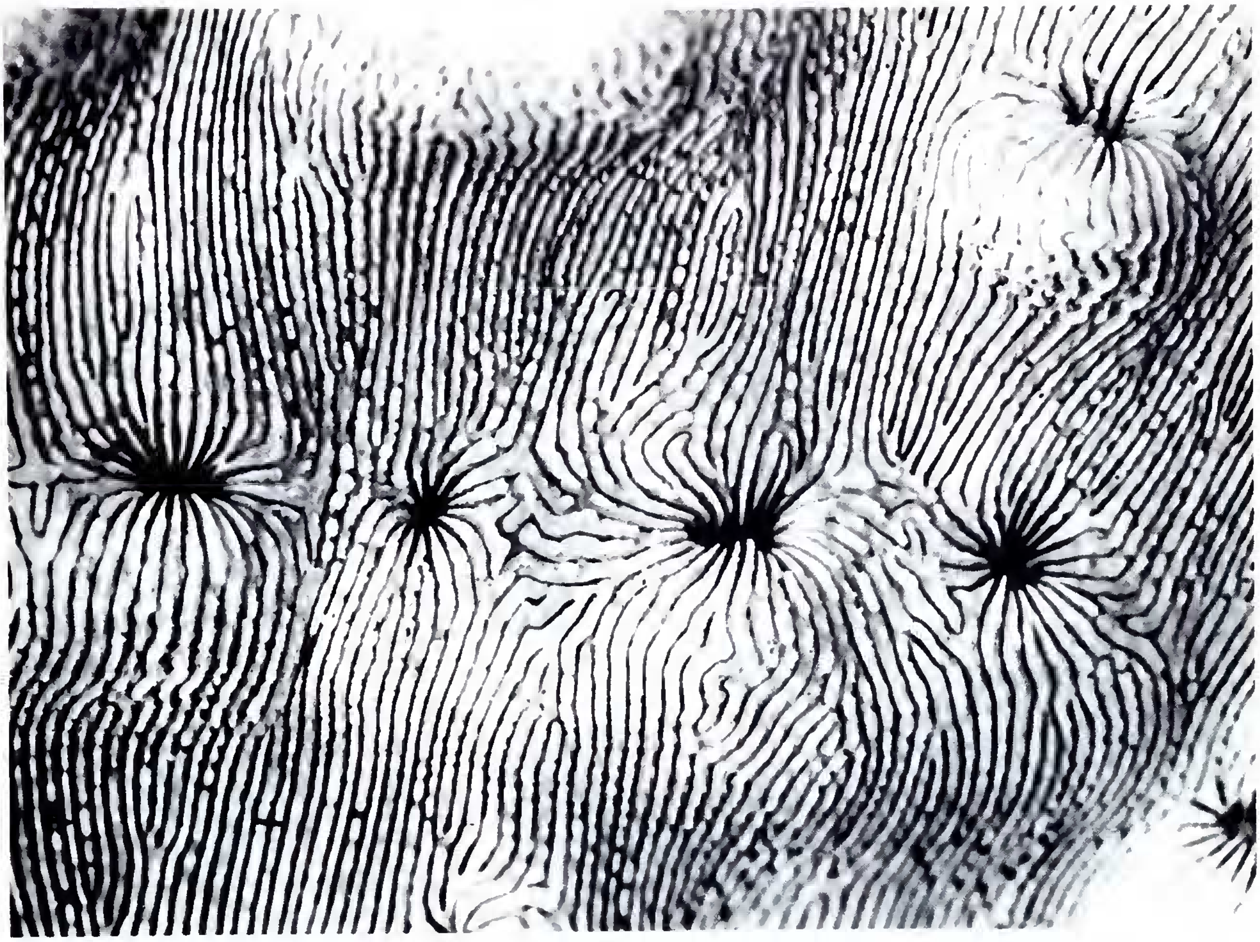
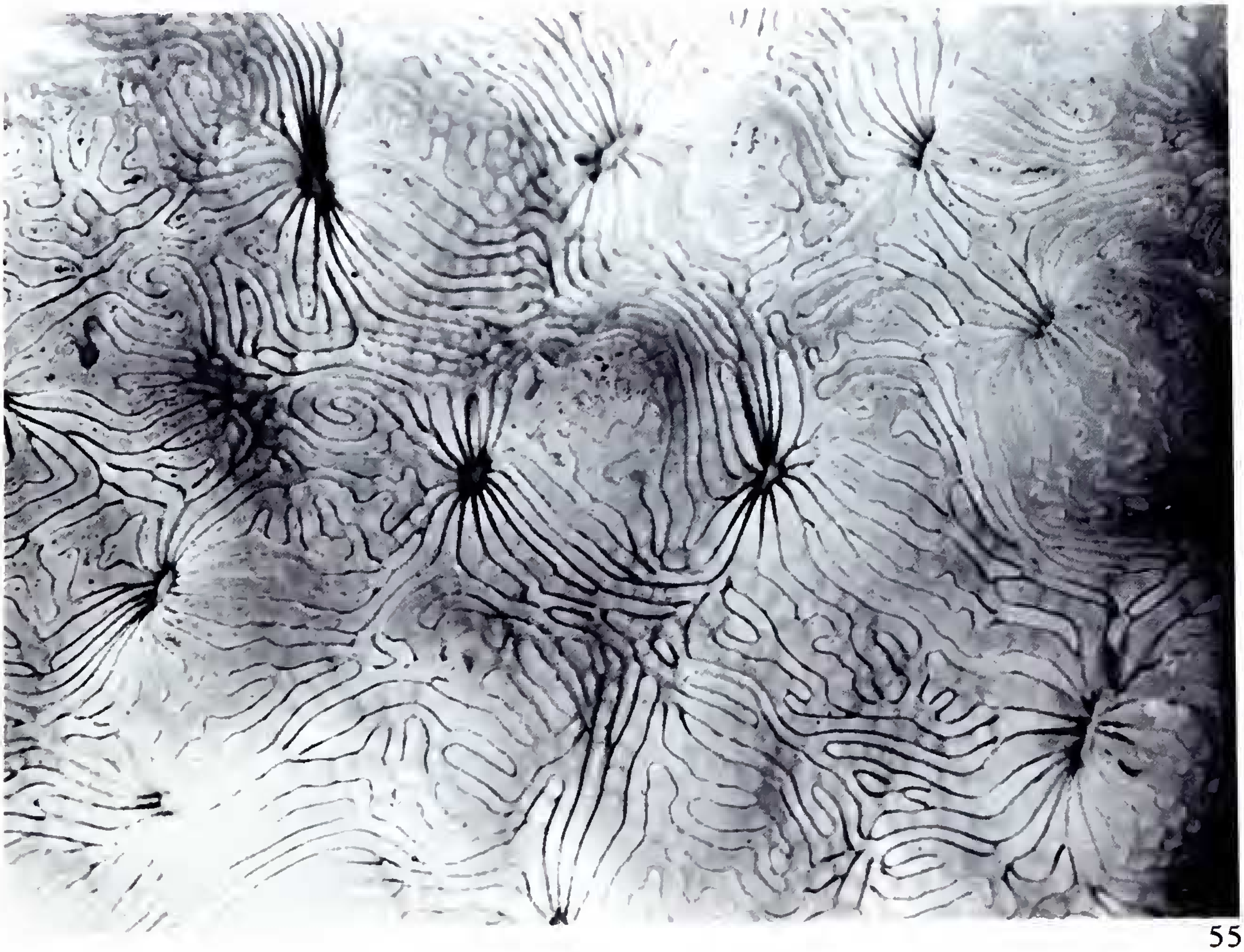



Fig. 95 ▲

Fig. 96 ▼



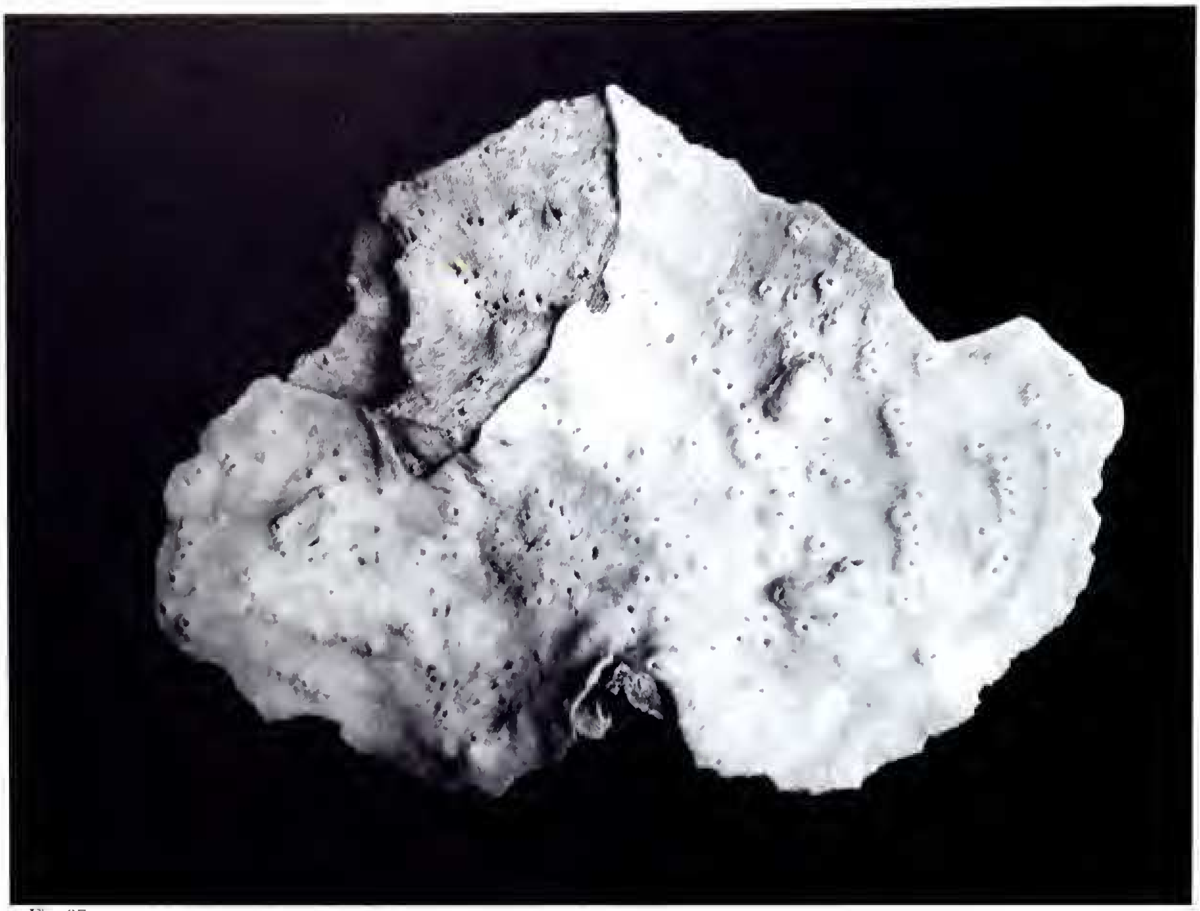
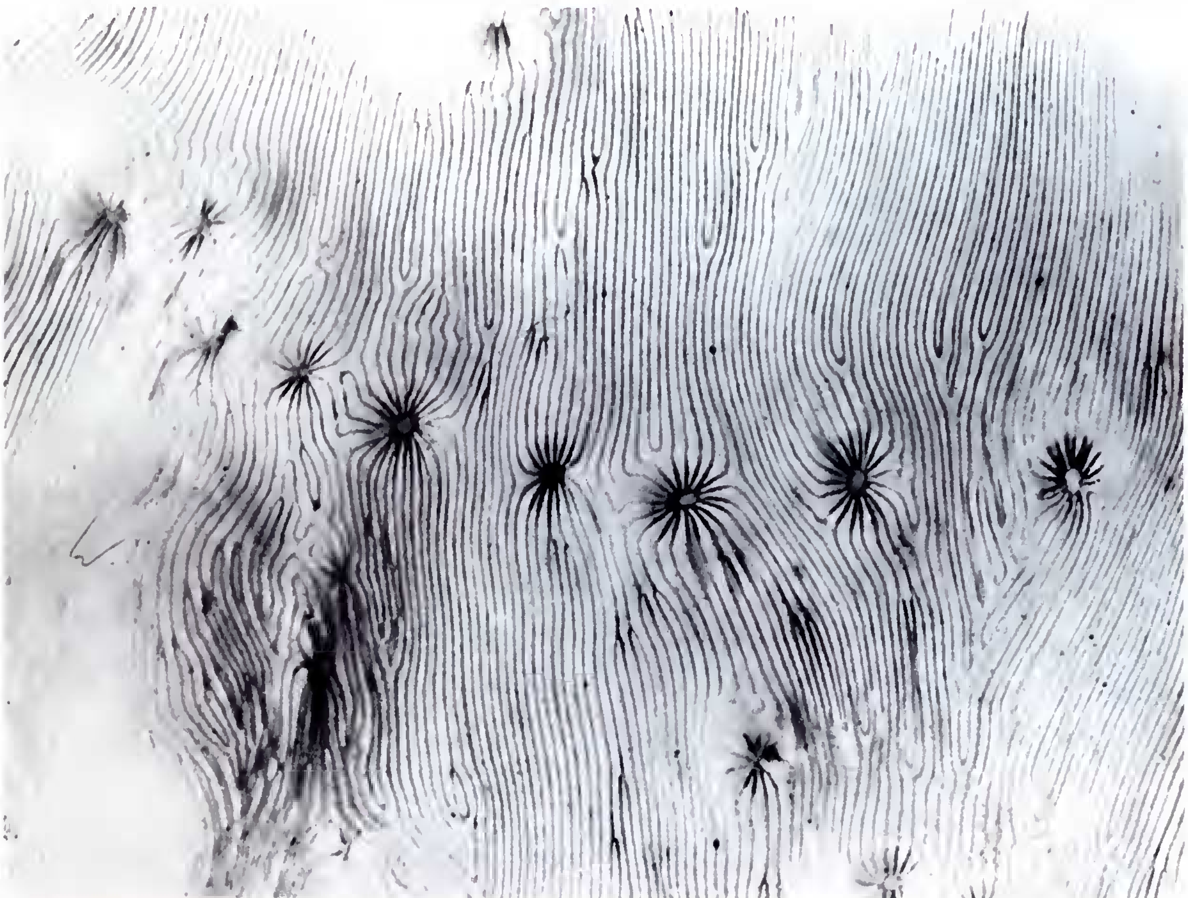


Fig. 97 ▲

Figs. 97, 98 Holotype of *Leptoseris hawaiiensis*, Fig. 97 (× 0.5), Fig. 98 (× 2.5).

Fig. 98 ▼



Most are tri-ridged, the lateral ridges bearing granules, the central ridge lobes or pinnacles, the latter frequently supporting fine horizontal dissepiments. Costae are mostly directional, running perpendicular to the margin, except in encrusting coralla or near the centre of laminar coralla where they may branch and be strongly crenellated. Calices are deep, the columellae small and compact. Backs of coralla are finely costate.

Of the present series, some specimens from Lord Howe Island, the southern known limit of *Leptoseris*, are closest to the type series from Hawaii. They differ primarily in having more heavily ornamented costae.

Living colonies (Fig. 740) are brown or green in colour.

Affinities

Leptoseris hawaiiensis closely resembles only the more abundant *L. scabra* (see p. 52).

Distribution

This species is apparently widespread although verified records are few. Its recorded range is from the Mascarene Archipelago in the west (Faure, 1976), the Andaman Islands, Indonesia, Palau, the Marshall Islands and Hawaii in the east.

Leptoseris mycetoseroides Wells, 1954

Synonymy

Agaricia? minikoiensis Yabe, Sugiyama & Eguchi (1936).

Agariciella ponderosa (Gardiner); Ma (1937).

Leptoseris mycetoseroides Wells, 1954; Pichon (1964); Scheer (1972).

Material studied

Bramble Cay (2 specimens), **Black Rocks** (3 specimens), **York Island, Darnley Island, Warrior Reef** (2 specimens), barrier reef NE of **Murray Islands** (2 specimens), **Murray Islands** (5 specimens), **Ashmore Reef, Great Detached Reef** (2 specimens), **Tijou Reef** (8 specimens), **Jewell Reef** (6 specimens), **Lizard Island** (6 specimens), **Yonge Reef** (3 specimens), **Palm Islands** (11 specimens), **Bowl Reef, Whitsunday Islands** (2 specimens), **Bushy Island-Redbill Reef, Pompey Complex, Swain Reefs** (5 specimens).

These localities include collecting stations 1, 2, 3, 7, 9, 10, 13, 28, 29, 32, 33, 34, 36, 38, 39, 42, 43, 51, 56, 61, 69, 79, 80, 81, 91, 96, 105, 107, 109, 120, 121, 126, 127, 128, 130.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are primarily encrusting, usually with free laminar margins (Fig. 741). They may be up to 2 m across and sometimes consist of several tiered plates (Fig. 103). There is relatively little variation in skeletal characters. Coralla with well developed, contorted carinae (Fig. 102) have calices grouped in short, irregular series.

Figs. 99-102 *Leptoseris mycetoseroides* Figs. 99, 100 (× 5.0), Figs. 101, 102 (× 2.5).

Fig. 99	From Curacao Island, Palm Islands, collecting station 56.
Figs. 100, 101	From Jewell Reef.
Fig. 102	From Maer Island, Murray Islands, collecting station 29.

Fig. 99 ▲

Fig. 100 ▼

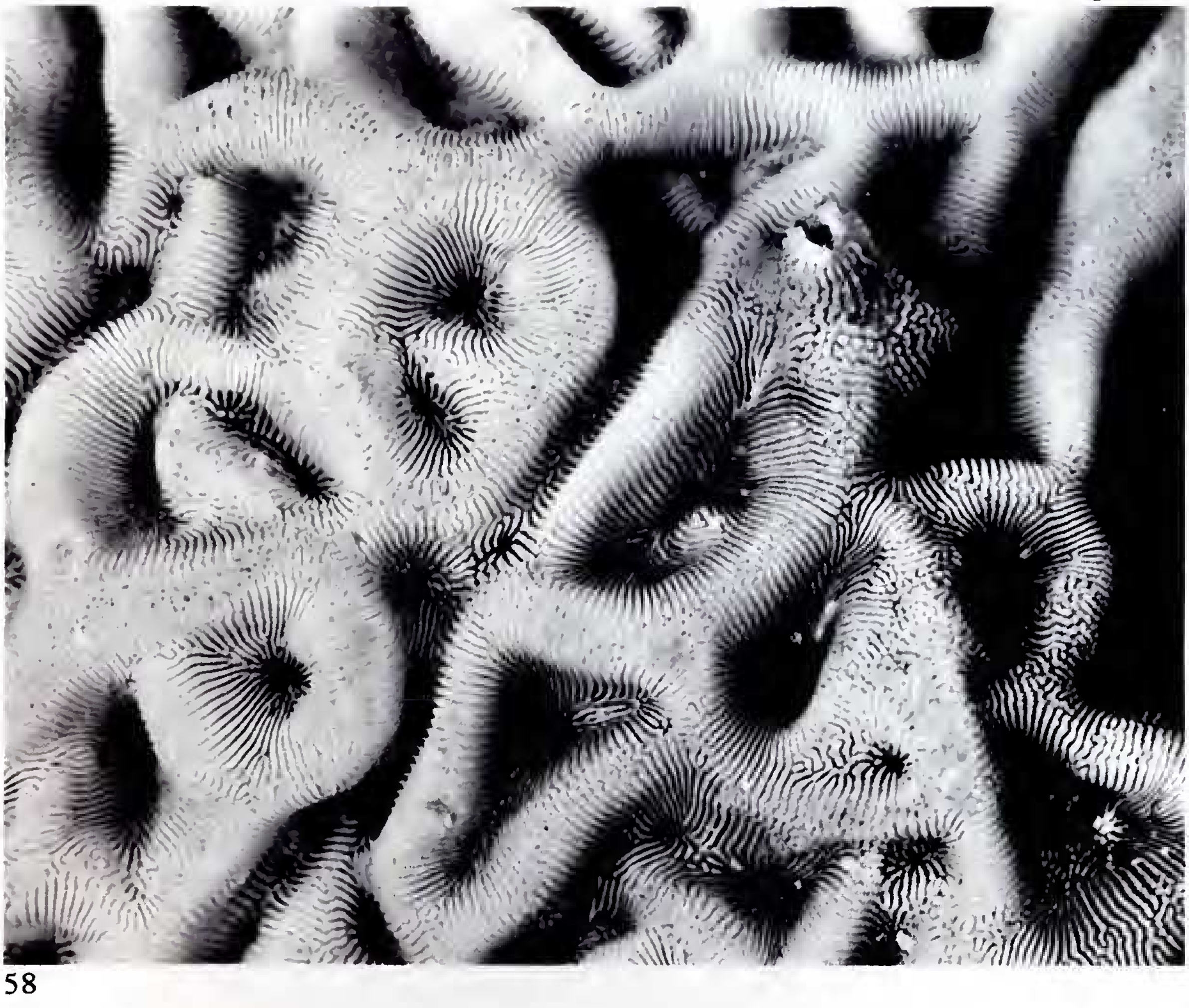


Fig. 101 ▲

Fig. 102 ▼

Fig. 103 *Leptoseris mycetoseroides* from Lord Howe Island.

Where carinae are more regularly concentric, extended *Pachyseris*-like rows of calices develop (Fig. 99). Calices do not have well defined thecae. Septo-costae are fine, regular and densely packed. They are usually arranged in two alternating orders. Rarely are they equal. First order septo-costae are slightly more exsert, either at the tops of the carinae or around the calice margins, and are more granulated and extend further towards the columellae. The columellae are likewise very variable and may be small and pinnacle-shaped or prominent and plate-like.

Living colonies (Fig. 742) are uniform or mottled brown and green. The colour becomes markedly darker as access to light decreases.

Affinities

As previously noted, *L. mycetoseroides* and *L. tenuis* have virtually identical septo-costae and must be distinguished on other characters (see p. 68). Differences between *L. mycetoseroides* and *L. yabei* are described below (p. 65).

In his original descriptions, Wells noted that this species also shows resemblances to *Pachyseris, Agaricia* and *Pavona.* The development of concentric carinae and plate-like columellae may be especially *Pachyseris*-like. Colonies with irregular carinae may also closely resemble *Gardineroseris,* which also has fine, closely packed septa. Wells further notes a resemblance to the Oligocene genus *Mycetoseris* 'which seems to represent the stock from which *Pavona, Agaricia, Pachyseris* and *Leptoseris* developed . . .'.

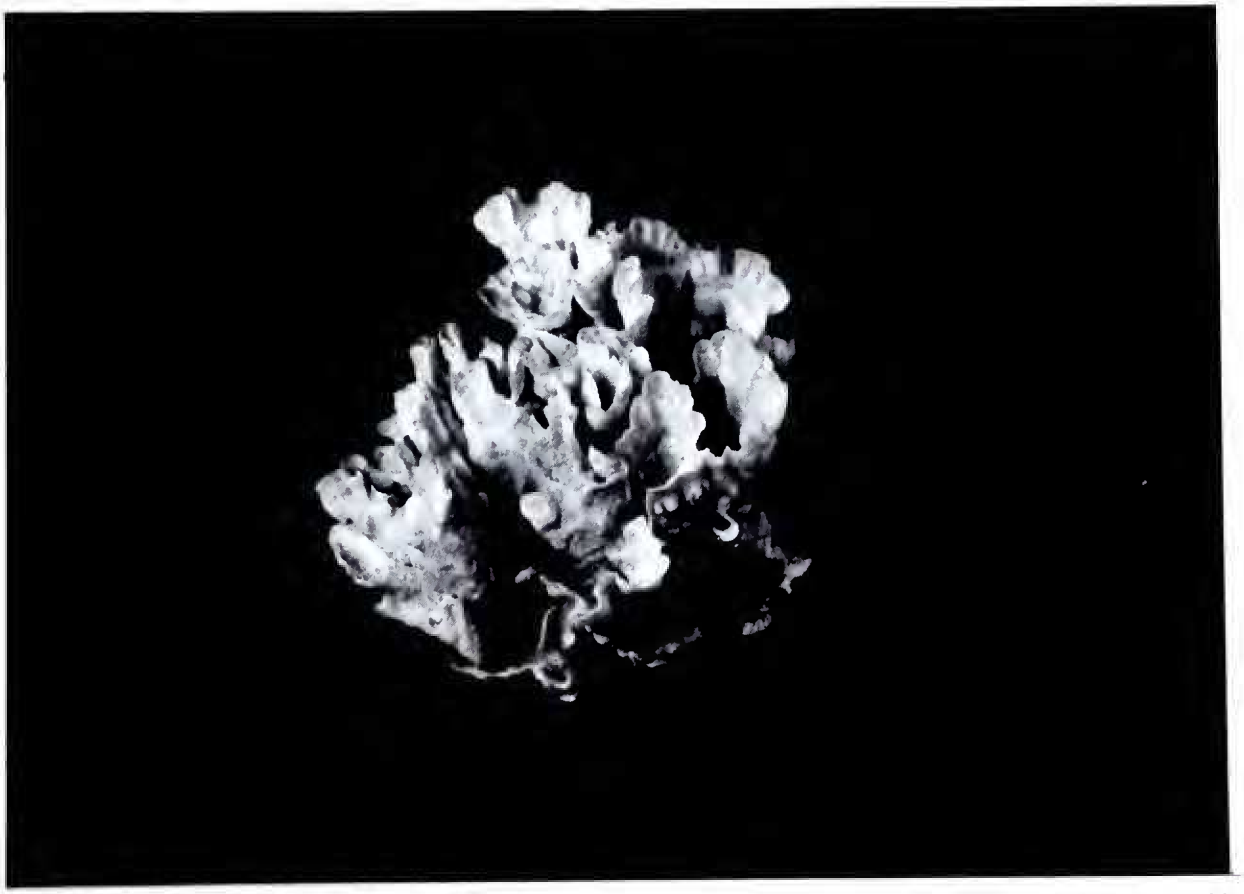
Distribution

Probably widely distributed but only previously recorded from Madagascar, Maldive Islands, Kyūshū, Honshū, and the Marshall Islands.

Fig. 104 ▲

Figs. 104, 105 *Leptoseris yabei* from Eclipse Island, Palm Islands, collecting station 59.

Fig. 105 ▼



Leptoseris yabei (Pillai & Scheer, 1976)

Synonymy

Pavona yabei Pillai & Scheer, 1976.

The holotype is the only previously recorded specimen of this species. Its generic position is changed because of a general similarity between the species and *L. mycetoseroides* and *L. tenuis* (see below) and because coralla form unifacial fronds with superficial calices inclined towards the margins. Alternatively, there is a good case for grouping these species into a separate genus.

Material studied

Bramble Cay, Anchor Cay, Darnley Island, Big Mary Reef, Yorke Island (8 specimens), **Warrior Reef, Murray Islands** (8 specimens), **Jewell Reef** (3 specimens), **Lizard Island** (2 specimens), **Ribbon Reef, Low Isles, Palm Islands** (26 specimens), **Whitsunday Islands** (2 specimens), **Swain Reefs** (4 specimens), **Wistari Reef.**

These localities include collecting stations 7, 12, 13, 28, 30, 32, 34, 35, 37, 38, 41, 42, 45, 55, 58, 59, 65, 78, 79, 81, 83, 90, 91, 92, 97, 98, 118, 121, 125, 126, 128, 129, 130, 131.

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies are mostly laminar. They commonly occur as plates with a vertical to horizontal orientation, or as a series of plates arranged in overlapping tiers (Fig. 744) frequently with upturned margins (Fig. 112). Occasionally colonies become vase-shaped, with a continuous lamina, or with two or more overlapping laminae. Large colonies frequently have combinations of several growth forms, frequently with horizontal plates at the bottom and near vertical, vase-shaped plates at the top (Fig. 104, 105). Except where adjacent fronds fuse, this species is unifacial with calices only on the upper or inner sides of laminae. However, highly folded colonies forming fluted tubes may have calices on the outer face.

Colonies of any growth form usually have well developed carinae, in roughly concentric rows, and well developed collines forming radiating ridges. The various degrees of development of those carinae and collines mostly dictate the shape and appearance of the calices. Coralla with well developed radiating collines (Fig. 106) have calices clumped into small groups and in extreme conditions have calices arranged in radiating rows between the collines. Frequently, well developed carinae and collines are found together, grouping the calices into square or rectangular pits.

Calices are usually inclined towards the corallum margins. Thecae are absent. Septo-costae are in two alternate orders. Those of the first order are thicker, more exsert, more granulated, extend further towards the columellae, and have steeper inner margins than those of the second order. The latter usually have evenly aligned inner margins. The majority of septo-costae are parallel to the collines. Columellae

Figs. 106-111 *Leptoseris yabei*, Figs. 107-111 (× 5.0).

Fig. 106 From Eclipse Island, Palm Islands, collecting station 59 (× 2.5).
Fig. 107 From Lizard Island, collecting station 32.
Fig. 108 From Pelorus Island, Palm Islands, collecting station 90.
Fig. 109 From the Swain Reefs, collecting station 79.
Fig. 110 From Jewell Reef.
Fig. 111 From Great Palm Island, collecting station 38.

Fig. 106 ▲

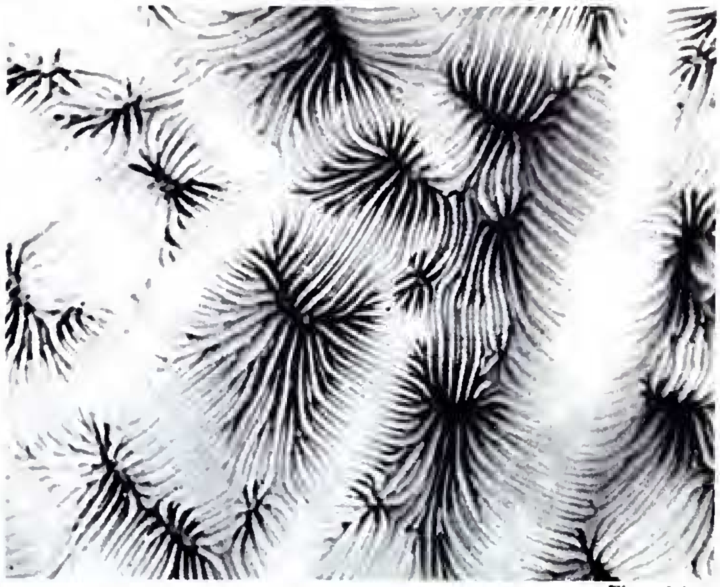


Fig. 107 ▲

Fig. 108 ▲

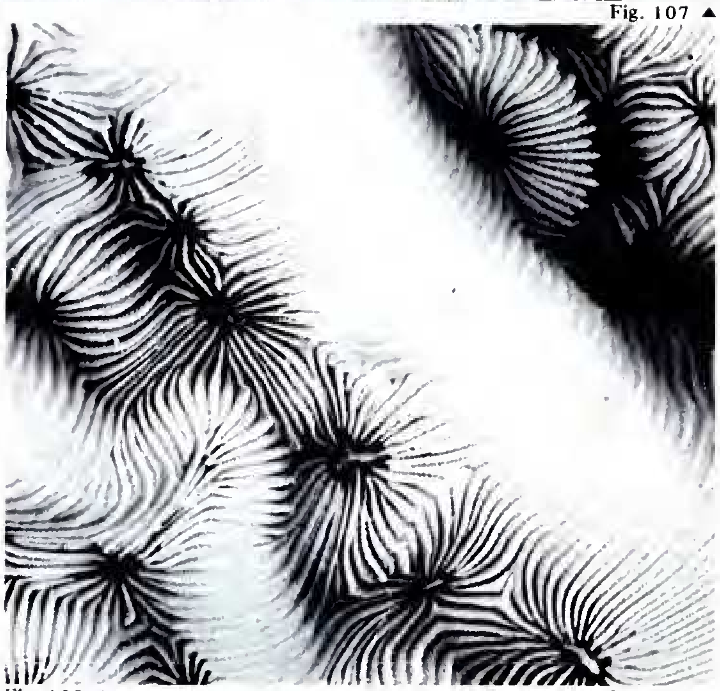


Fig. 109 ▲

Fig. 110 ▼

Fig. 111 ▼

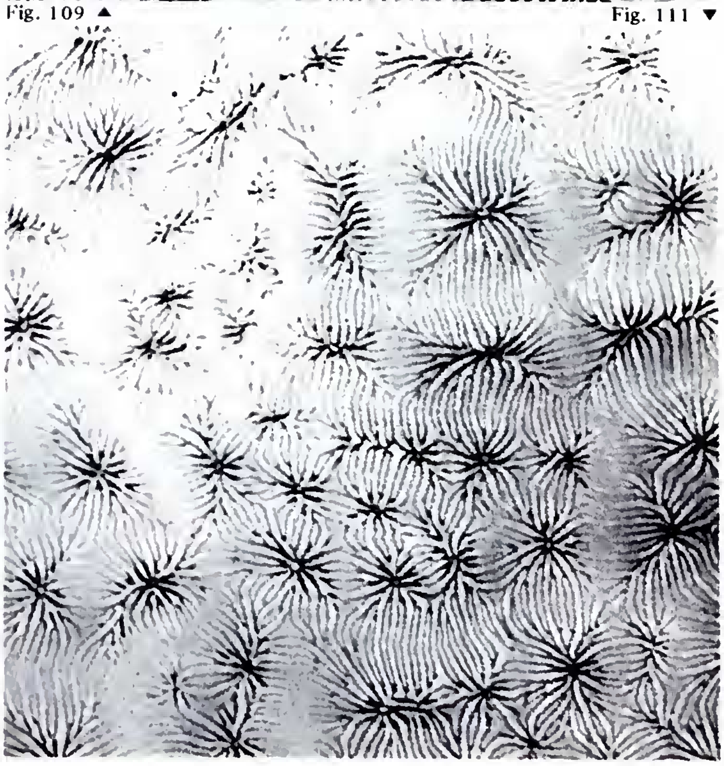


Fig. 112 ▲

Figs. 112-114 *Leptoseris yabei.*

Fig. 112 From the Swain Reefs.
Figs. 113, 114 From Eclipse Island, Palm Islands, collecting station 59.

Fig. 113 ▼

Fig. 114 ▲

are pinnacle or plate-like. The undersurfaces of laminae are finely costate and folded, the folds corresponding to the collines.

Living colonies (Figs. 743, 744) are mostly pale brown or yellow.

Affinities

This species is closest to *L. mycetoseroides* although it is usually readily distinguished by the presence of radiating collines. Parts of coralla which are submassive or encrusting without radiating collines are distinguished from *L. mycetoseroides* and *L. tenuis* by having thinner, less granular and more strongly alternating septo-costae.

Distribution

Previously recorded only from the Maldive Islands.

Leptoseris tenuis van der Horst, 1921

Synonymy

Leptoseris tenuis van der Horst, 1921; van der Horst (1922a); Yabe & Sugiyama (1941); Ma (1959).

Material studied

Big Mary Reef (2 specimens), **Yorke Island, Ashmore Reef** (4 specimens), **Palm Islands** (3 specimens), **Whitsunday Islands** (2 specimens).

These localities include collecting stations 45, 59, 98, 107, 117, 125, 131, 143.

Fig. 115 ▲

Figs. 115, 116 *Leptoseris tenuis* from Big Mary Reef, collecting station 131 (× 2.5).

Fig. 116 ▼

Previous records from Eastern Australia

Not previously recorded.

Characters

Small colonies are encrusting as are the specimens of van der Horst and Yabe & Sugiyama. Larger colonies (Figs. 115, 116) are encrusting or submassive or have free margins developing into unifacial laminae which are usually flat and horizontal but which may become upright and foliaceous. Calices are irregularly distributed or, in laminar coralla, are arranged in rows concentric with the margins. These rows are separated by low carinae. Calices are superficial with little or no development of thecae. The columellae, which consist of one or several pinnules or are plate-like, are

Figs. 117-120 *Leptoseris tenuis* (× 0.5).

Fig. 117	From Big Mary Reef, same corallum as Fig. 115.
Fig. 118	From Ashmore Reef, collecting station 107.
Figs. 119, 120	From Big Mary Reef, same corallum as Fig. 116.

Fig. 117 ▲

Fig. 118 ▲

Fig. 119 ▼

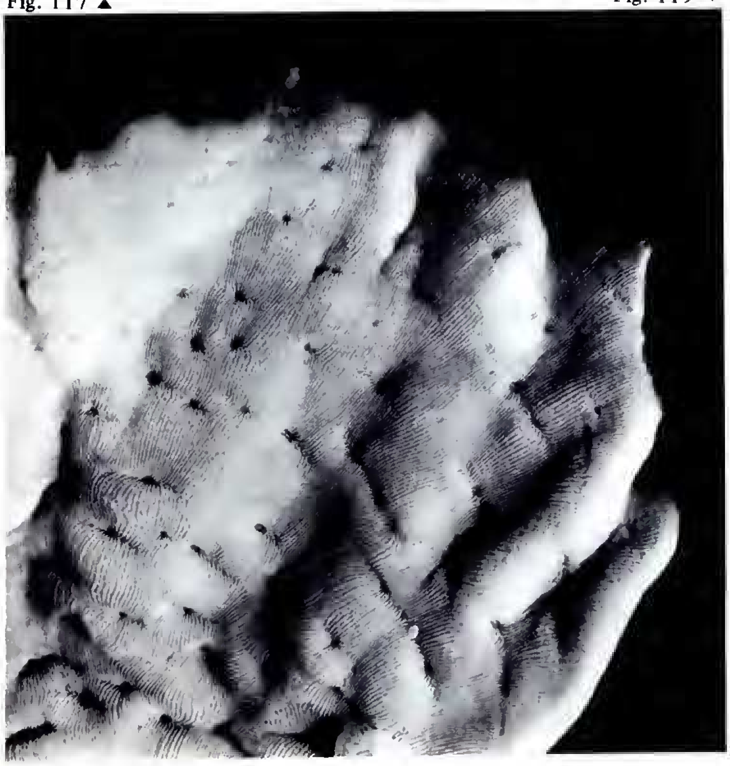
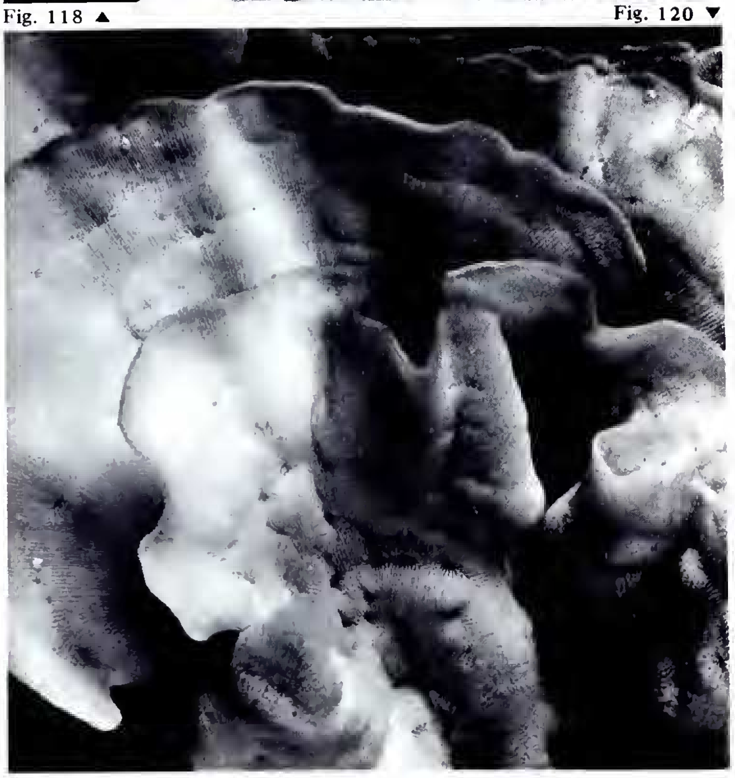


Fig. 120 ▼



conspicuous. Septa have free, vertical, inner margins. Costae are fine, equal or slightly alternate. They are closely spaced and heavily granulated giving coralla a smooth appearance. They are usually straight but may be highly crenellated and branched. The undersurface of laminae are smooth or very finely costate.

Affinities

Leptoseris tenuis has close affinities with *L. yabei* and, particularly, with *L. mycetoseroides*, although it is easily distinguished from them. Foliaceous colonies of *L. tenuis* may be similar to those of *L. yabei* but lack the radiating ridges and the alternate, relatively widely spaced septa of *L. yabei*, allowing even small pieces of coralla to be readily distinguished. *Leptoseris mycetoseroides* and *L. tenuis* have virtually identical septo-costae. The former is distinguished by its relatively prominent carinae and more deeply seated calices and by its primarily encrusting growth form.

Distribution

Previous records are from the Amirante and Providence Islands in the western Indian Ocean and the Solomon and Paternoster Islands of the western Pacific.

GENUS *GARDINEROSERIS* SCHEER & PILLAI, 1974

Generic synonymy

Asteroseris Verrill, 1901 (*non Asteroseris* de Fromentel, 1867).

Agariciella Ma, 1937.

Gardineroseris Scheer & Pillai, 1974.

Type species *Agaricia ponderosa* Gardiner, 1905.

Gardineroseris is a distinct monospecific genus with its only species originally described by Dana (1846) as *Agaricia planulata.* In 1901 Verrill created the genus *Asteroseris* to distinguish this Pacific form from West Indian species. Because this name was pre-occupied, it was never subsequently used. In 1905, Gardiner described *Agaricia ponderosa* with a variety *minikoiensis.* Yabe *et al.* (1936) described a different species (*Leptoseris mycetoseroides*) as *Agaricia* (?) *minikoiensis* (Gardiner) claiming this to be distinct from *A. ponderosa.* Ma (1937) subsequently created the subgenus *Agariciella* (of *Agaricia*) on the specimens of Yabe *et al.* although he later dropped this name. The genus *Agariciella* therefore, is not based on either variety of Gardiner's species.

Scheer & Pillai (1974) proposed the name *Gardineroseris* for one of Gardiner's varieties and claimed that the other, var. *minikoiensis*, was generically distinct, and should be retained as the type species of *Agariciella.*

This study supports the conclusion of Wells (1936) that *A. planulata* Dana and *A. ponderosa* Gardiner are the same species and shows conclusively that the two varieties of the latter are conspecific, var. *minikoiensis* simply being the form normally found around the margins of otherwise typical *ponderosa*-like colonies. The same conclusion was also made by Wells (pers. comm.). The genus *Gardineroseris*, however, is retained as the only available generic name for Dana's original species.

Gardineroseris planulata (Dana, 1846)

Synonymy

Agaricia planulata Dana, 1846; Edwards & Haime (1860).

Asteroseris planulata (Dana); Verrill (1901).

Agaricia ponderosa Gardiner, 1905; Vaughan (1918); van der Horst (1922a);

Faustino (1927); (*pars*) Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Ma (1959); Pichon (1964).

Agaricia ponderosa var. *minikoiensis* Gardiner, 1905.

Pavona (Polyastra) planulata (Dana); Wells (1936a); Chevalier (1968).

Pavona (Polyastra) ponderosa (Gardiner); Matthai (1948b); Durham (1962).

Gardineroseris ponderosa (Gardiner); Scheer & Pillai (1974).

Material studied

Yorke Island (6 specimens), **Warrior Reef, Dungeness Island,** reef 8 km NE **Murray Islands** (2 specimens), **Murray Islands** (3 specimens), **Aureed Island, Tijou Reef** (2 specimens), **Lizard Island** (3 specimens), **Yonge Reef** (4 specimens), **Ribbon Reef, Hope Island** (2 specimens), **Fitzroy Island, Palm Islands** (5 specimens), **Bushy Island-Redbill Reef, Pompey Complex, Wistari Reef.**

These locations include collecting stations 2, 7, 9, 13, 26, 28, 32, 33, 37, 65, 90, 92, 105, 117, 121, 122, 125, 133, 139.

Previous records from Eastern Australia

Not previously recorded.

Characters

Small colonies are encrusting with laminar edges; larger colonies become massive (Fig. 745), frequently columnar (Fig. 121). The surface of coralla are regularly undulated and consist of valleys or pits of variable shape, approximately 3 mm deep and usually <7 mm maximum dimension. These pits are separated by high collines. They contain 1-5 centres, usually one in the case of parts of colonies undergoing little or no growth. In early stages of division these centres are linked by trabecular linkages only. Thin thecae and increasing numbers of septa subsequently develop which

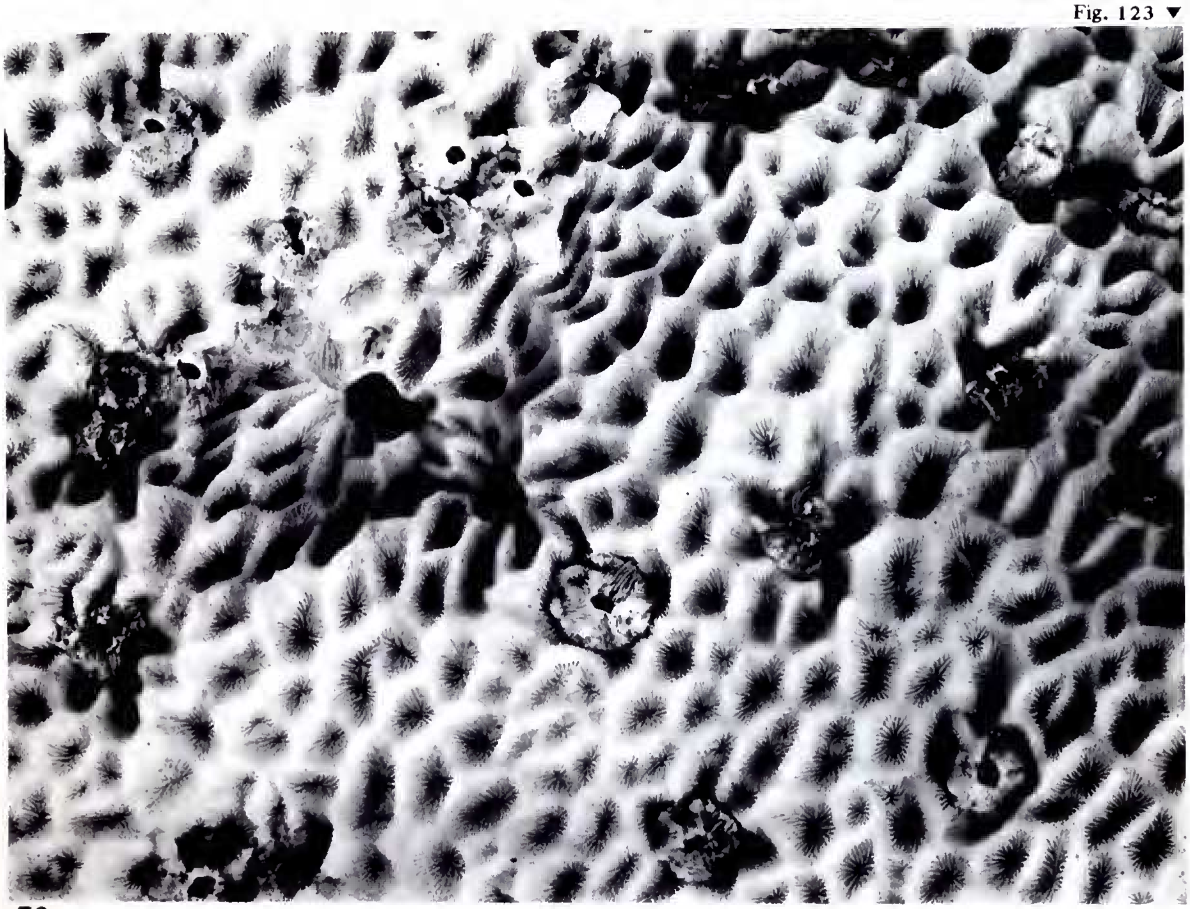
Fig. 121 *Gardineroseris planulata* from Elk Cliff, Great Palm Island, collecting station 37 (× 0.5).

Fig. 122 ▲

Figs. 122-125 *Gardineroseris planulata* (× 2.5).

Fig. 122	From Dungeness Reef, collecting station 122.
Fig. 123	From Great Palm Island, same corallum as Fig. 121.
Figs. 124, 125	From Yorke Island, collecting station 13.

Fig. 123 ▼



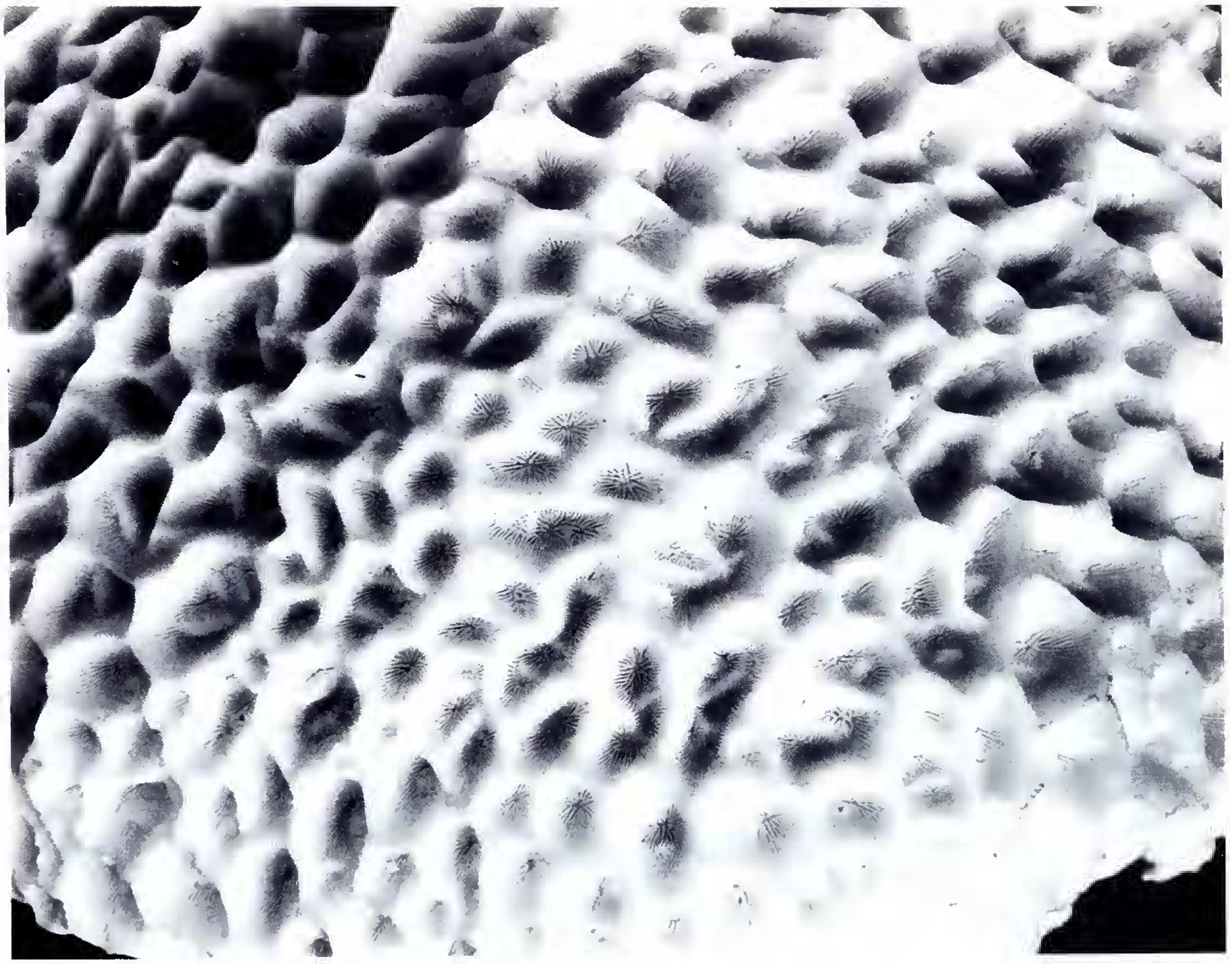


Fig. 124 ▲

Fig. 125 ▼

eventually give rise to a high colline. Budding occurs in almost any place on the pit floor or on the collines; thus, for actively growing surfaces, the collines are very uneven and reflect varying stages of development. Septa are pavonid in appearance except that they are always equally exsert. They are usually thin and always densely packed. They descend abruptly down the endotheca and are always very even. Two orders of septa are recognised in some coralla, the second order ending abruptly at the bottom of the collines where they have free margins. Usually <10 septa reach the columellae; most of those of the first order either anastomose or have free inner margins. All septa are covered with granules which may project outwards to 3 times the septal width and form pseudosynapticulae. The columellae are small and consist of a few fused trabeculae.

Laminar colonies have a smooth edge zone usually <10 mm wide. Living colonies are usually uniform in colour which varies from light to dark brown, purple or yellow. In some colonies the pits are darker than the collines.

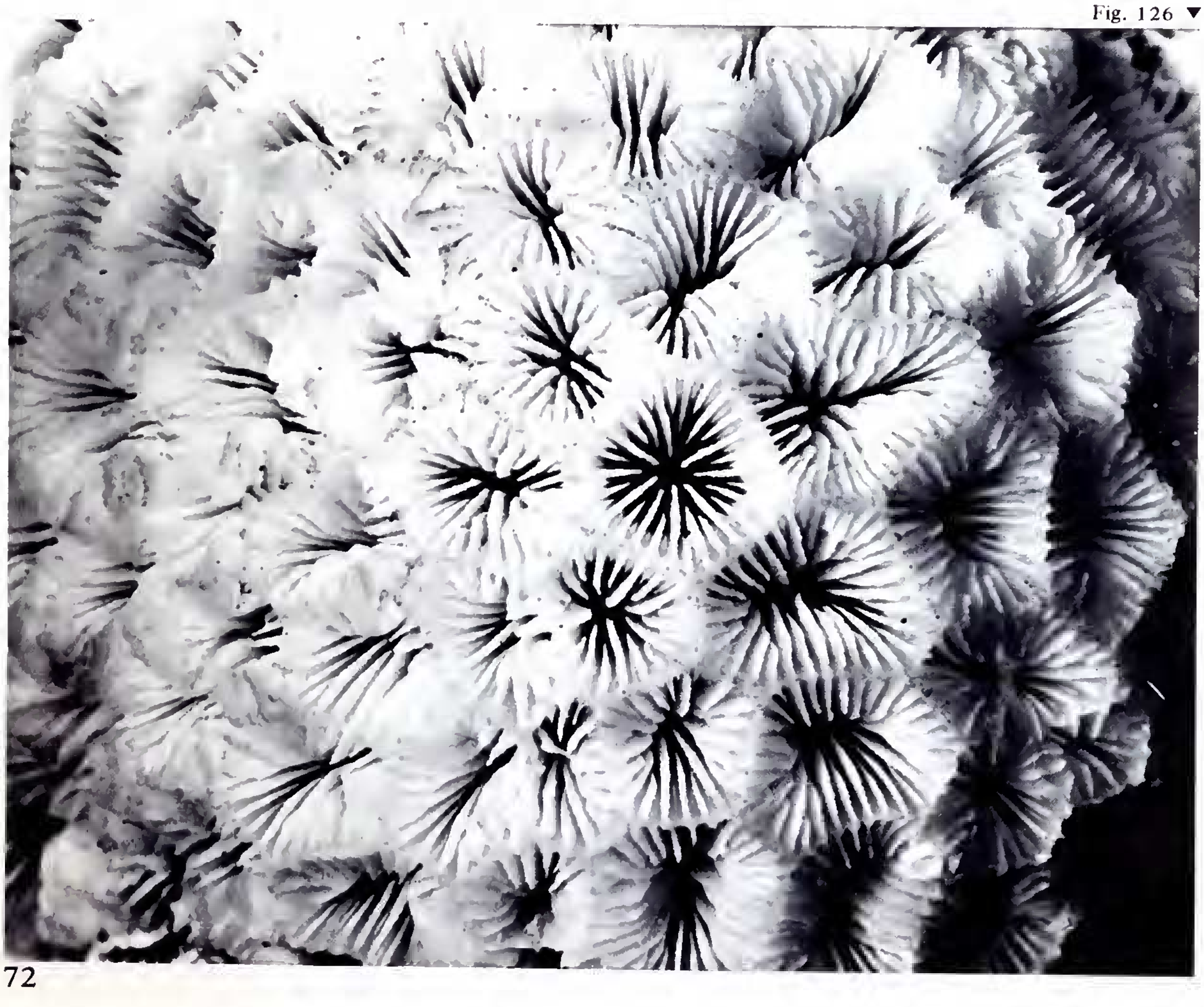
Distribution

Widely distributed from the Red Sea throughout the tropical Indo-Pacific east to the Marshall Islands.

Figs. 126-129 *Coeloseris mayeri* Figs. 126, 127 (× 5.0) Figs. 128, 129 (× 2.5)

Fig. 126 From Hope Island.
Fig. 127 From Bewick Island.
Fig. 128 From Juno Bay, Fantome Island, Palm Islands, collecting station 43.
Fig. 129 From Lizard Island, collecting station 33.
Fig. 130 *Coeloseris mayeri* from the Swain Reefs.

Fig. 126 ▼



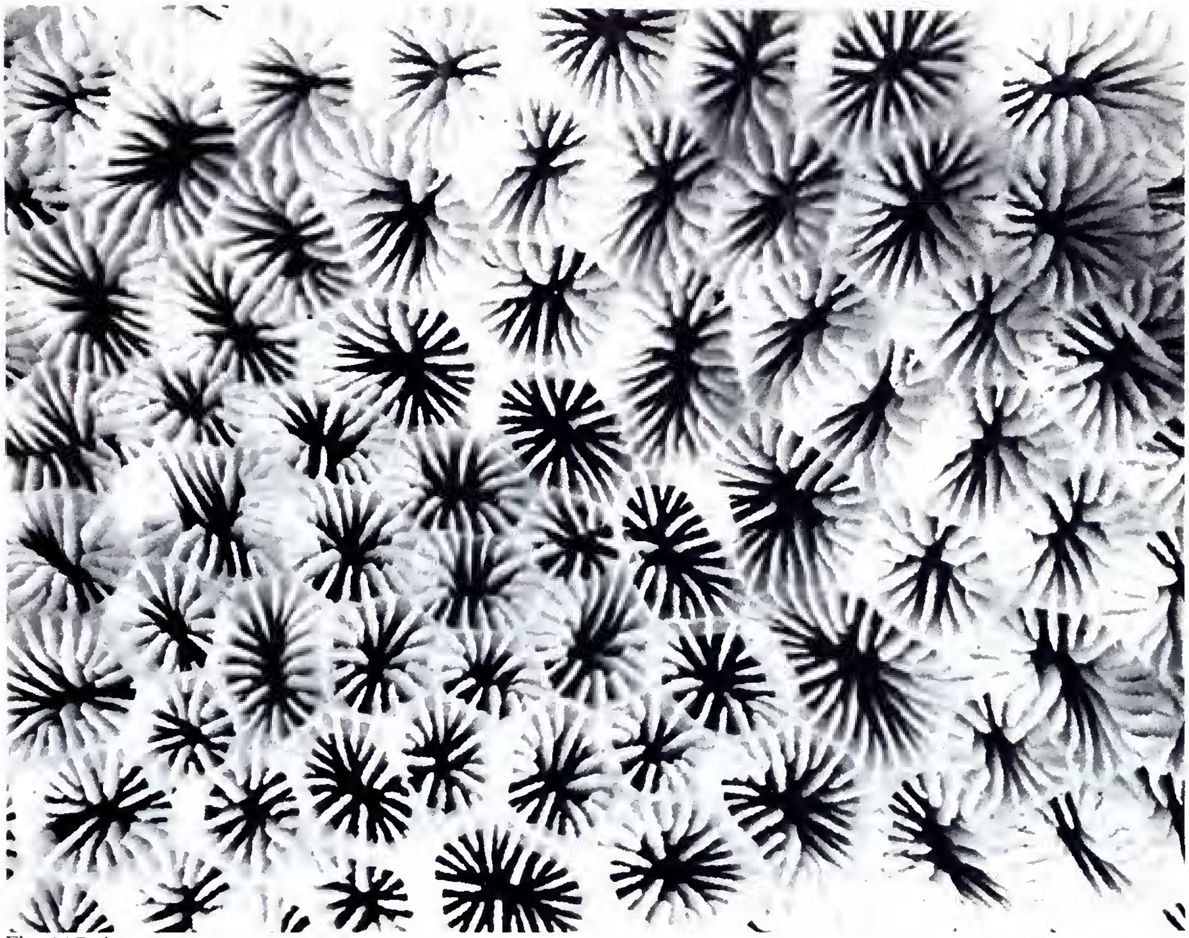
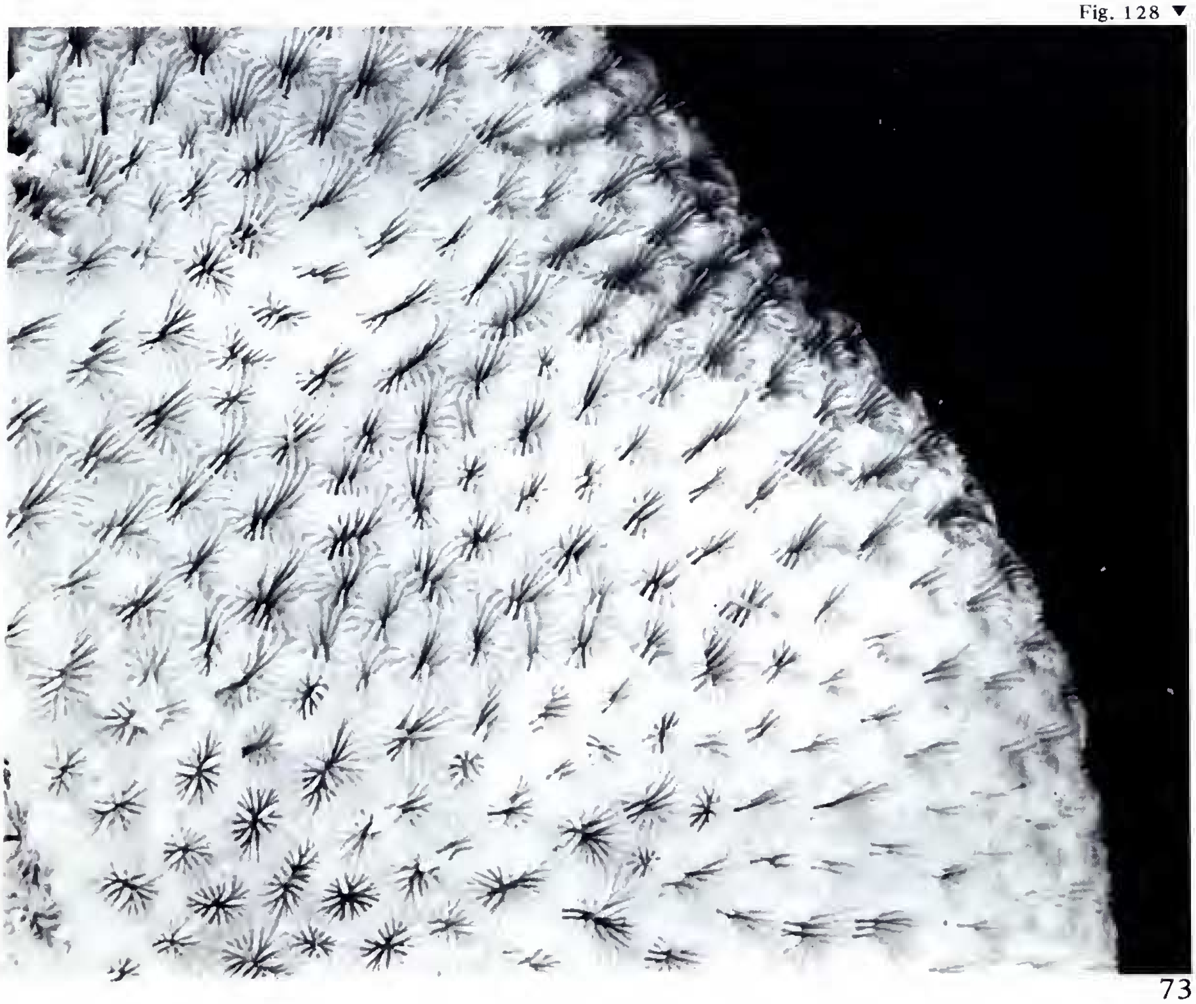


Fig. 127 ▲

Fig. 128 ▼



Generic synonymy

Coeloseris Vaughan, 1918.

Xishasiderastrea Zou, 1975b.

Type species *Coeloseris mayeri* Vaughan, 1918.

Characters of the genus

Coralla are cerioid with colonies formed by monostomodaeal budding. Columellae are absent and the axial space open.

Coeloseris mayeri Vaughan, 1918

Synonymy

Coeloseris mayeri Vaughan, 1918; Matthai (1924); Faustino (1927); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1939, 1940); Nemenzo (1955a); Crossland (1952); Chevalier (1968); Scheer & Pillai (1974).

Xishasiderastrea sinensis Zou, 1975b.

Xishasiderastrea granulata Zou, 1975b.

The two species described by Zou are distinguished primarily by the septa of *X. granulata* being 'armed with well marked granules, by means of which the septa of neighbouring calices are joined to each other'. A similar condition is found in parts of some *C. mayeri* coralla as noted below.

Fig. 129 ▼

Material studied

Reef NE from **Murray Islands, Murray Islands, Sue Island** (2 specimens), **Northwest Reef, Great Detached Reef** (4 specimens), **Bewick Island, Houghton Island, Jewell Reef, Lizard Island** (4 specimens), **Yonge Reef, Eyrie Reef, Hope Islands** (2 specimens), **Low Isles, Palm Islands** (5 specimens), **Keeper Reef, Swain Reefs.**

These localities include collecting stations 5, 7, 9, 11, 14, 17, 18, 19, 21, 33, 40, 43, 45, 77, 92, 99, 100.

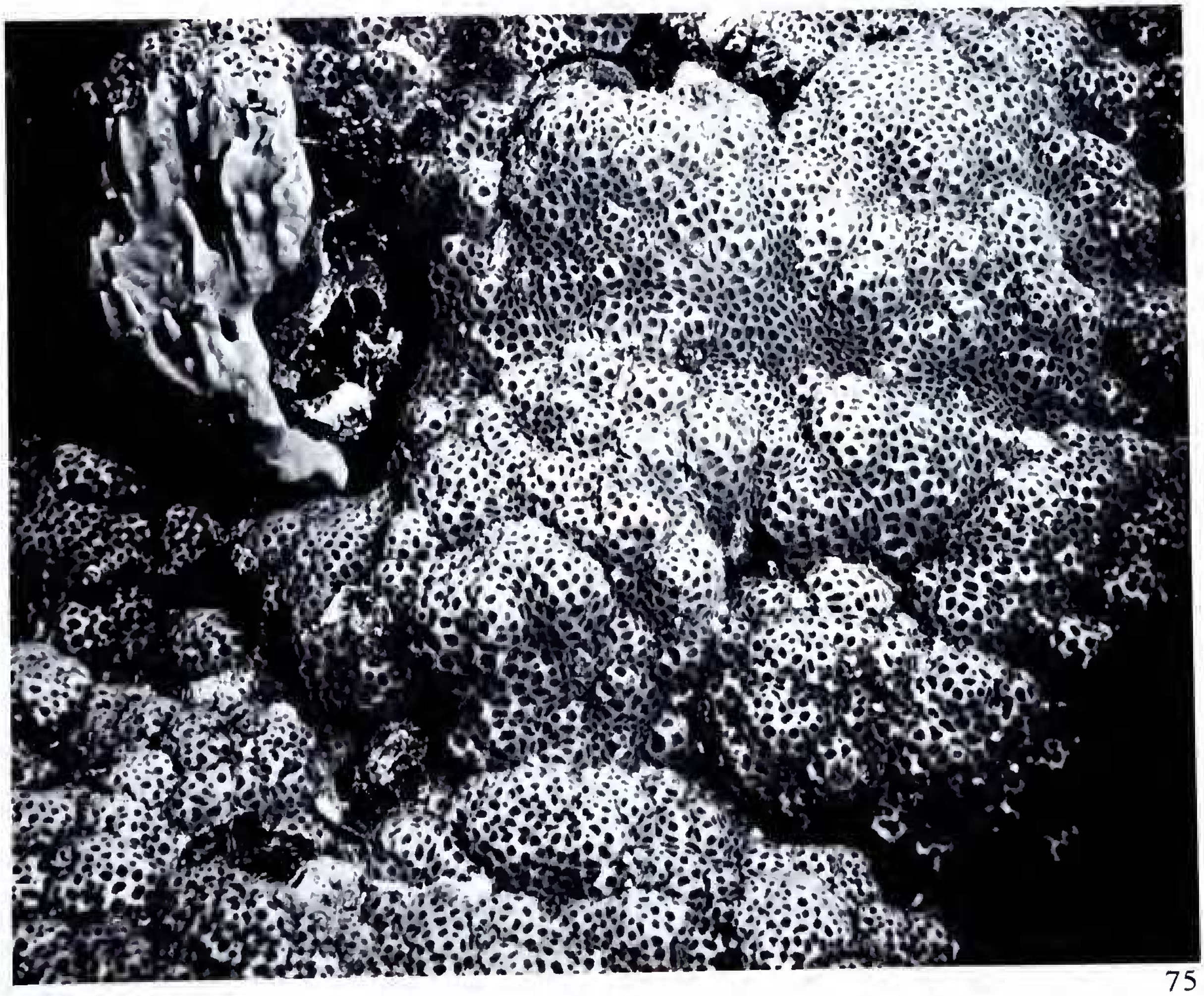
Previous records from Eastern Australia

Murray Islands, Vaughan (1918), Mayor (1918), Yonge (1930, 1940), Crossland (1952).

Characters

Colonies are massive and cerioid with undulating surfaces which may form hillocks or columns (Fig. 130). Calices are polygonal, average approximately 6 mm diameter and show relatively little variation. Septa are arranged in three orders, the third order being abortive. In some coralla the orders are not readily distinguished. First and second order septa are evenly exsert with those of adjacent corallites adjoined except where the common wall is very acute and septothecate. The inner margins of first order septa are sub-vertical and plunge into deep calices; their upper margins are frequently horizontal. Septa are usually finely granulated. There are no columellae. The common wall may be up to 5 mm thick and rounded but is usually thinner and acute. In the latter case there may be a fine inter-septal ridge above the theca. Budding is both intra- and extra-tentacular.

Fig. 130 ▼



Living colonies are usually pale green, yellow or brown, with darker calices. The margins of exsert septa are sometimes white (Fig.746). This species is abundant and readily distinguished underwater.

Affinities

Coeloseris is a monospecific genus which has no clear affinities. Septa are primarily pavonid in appearance and come closest to *P. minuta.* In other respects *Coeloseris* shows similarities with *Siderastrea* but lacks the characteristic synapticular rings of *Siderastrea* and has no columellae.

Distribution

Previous records indicate a restricted distribution from the Nicobar Islands in the west to New Caledonia in the east.

GENUS *PACHYSERIS* EDWARDS & HAIME, 1849

Generic synonymy

Agaricia (*pars*) Lamarck (1816), (*pars*) Dana (1846).

Pachyseris Edwards & Haime (1849c).

Type species *Agaricia rugosa* Lamarck, 1801.

Characters

Colonies are laminar and unifacial to branching and bifacial. Calices are indistinct and minute and are in approximately concentric rows separated by carinae. Thecae are seldom distinguished. Septo-costae are pavonid in structure but do not radiate from centres.

The two species of *Pachyseris* from the Great Barrier Reef are readily distinguished. One, *P. rugosa*, has a wide range of growth forms and skeletal characters, and includes most of the 12 nominal species of the genus.

Pachyseris rugosa (Lamarck, 1801)

Synonymy

Agaricia rugosa Lamarck, 1816; Dana (1846).

Pachyseris rugosa (Lamarck); Edwards & Haime (1851a, 1860); Duncan (1884); van der Horst (1921); Faustino (1927); Thiel (1932); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Umbgrove (1939); Matthai (1948a); Wells (1954); Nemenzo (1955a); Ma (1959); Pichon (1964); Chevalier (1968); Scheer & Pillai (1974).

Pachyseris valenciennesi Edwards & Haime, 1851a; Edwards & Haime (1860); Studer (1880); Duncan (1884); Ortmann (1888, 1889); van der Horst (1921, 1922a); Matthai (1948a).

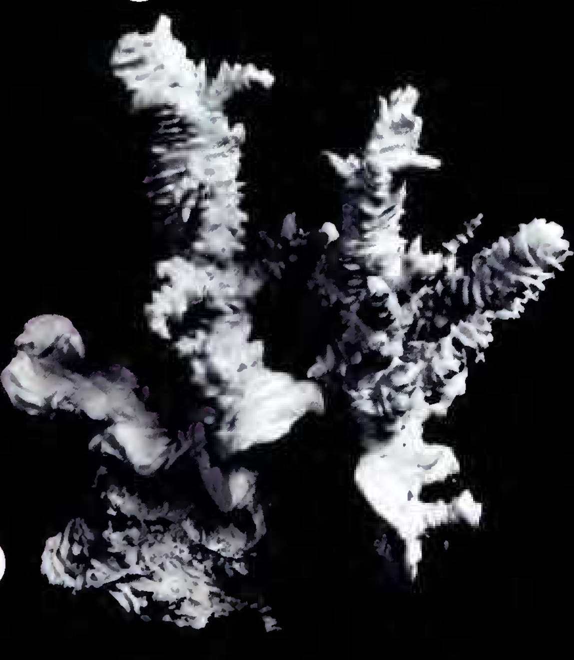
Pachyseris monticulosa Verrill, 1872; Verrill (1875); Studer (1901).

Figs. 131-134 *Pachyseris rugosa* (× 0.5).

Fig. 131 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.
Fig. 132 From Cateran Bay, Border Island, Whitsunday Islands, collecting station 101, showing close similarity with the holotype of *P. torresiana.*
Figs. 133, 134 From Sue Island, collecting station 17.

131

132



133

134

Pachyseris carinata Brüggemann, 1879b; van der Horst (1921); Hoffmeister (1925); Matthai (1948a); Ma (1959); Scheer (1972).

Pachyseris torresiana Vaughan, 1918; van der Horst (1921); Yabe & Sugiyama (1935a); Matthai (1948a); Crossland (1952).

Pachyseris gemmae Nemenzo, 1955a.

Pachyseris valenciennesi is a re-description of Dana's *Agaricia rugosa* and was claimed by Edwards & Haime (1851a) to differ from the latter by having equal, regular septa and a weakly developed columella. Van der Horst (1921) distinguishes *P. valenciennesi* as having 'a very irregular disc with hollow protuberances and folded and upturned edges' while *P. rugosa* 'consists of a more regular corallum attached by nearly all of its underside'. His figured specimen is similar to Vaughan's *P. torresiana.* Verrill (1872) proposed the name *P. monticulosa* for *P. rugosa* (just as Edward & Haime proposed the name *P. valenciennesi*).

The synonymy of *P. carinata* and *P. torresiana* with *P. rugosa* was suggested by van der Horst and supported by Nemenzo (1959) while Hoffmeister (1925) considered *P. carinata* a valid species with *P. torresiana* a synonym. He concluded that van der Horst's *P. rugosa* belonged to *P. carinata* but that *P. rugosa* (Lamarck) differs in having thin, distinctly alternating septa and a 'thin, irregular, undulating, explanate corallum'.

Pachyseris gemmae Nemenzo appears also to belong to this species as the illustrated growth form, and the skeletal characters as described, both fall within the normal range of *P. rugosa.*

Material studied

Dredged 3 km NW of barrier reef NE from **Murray Islands, Sue Island, Lizard Island, Low Isles** (3 specimens), **Palm Islands** (12 specimens), **Whitsunday Islands** (4 specimens), **Pompey Complex**.

These localities include collecting stations 17, 23, 32, 41, 45, 75, 90, 97, 98, 100.

Previous records from Eastern Australia

Torres Strait (as *P. torresiana*), Vaughan (1918); **Low Isles,** Stephenson & Wells (1955).

Characters

Small colonies are encrusting, initially with laminar edges which frequently form flat unifacial plates up to 20 cm across. These usually become thickened by upward growth and develop very irregular upper surfaces. Irregular vertical plates, ridges or columns develop which in larger colonies branch and anastomose (Figs. 131, 132, 747). Such colonies may grow to a very large size (>10 m diameter); these are usually dome-shaped (Figs. 135, 136).

Calices are arranged approximately concentric to the corallum centre or form horizontal rows traversing vertical branches or plates. Individual rows may be up to 10 cm long on flat surfaces but become increasingly shorter and less regular as the branching pattern of coralla becomes more complex. Individual corallites are spaced at irregular intervals of 1-1.5 mm and are frequently indistinct. Individual thecae are seldom distinguishable, the rows of corallites being separated by carinae which may vary greatly in shape within the one corallum. Those at the base of large coralla are usually low and broad (up to 4 mm); they usually become increasingly acute on the branches with straight, convex or concave sides. Many coralla have carinae with one gently sloping face, the other vertical or overhung. Calice centres are usually arranged in exact rows along the valley axes but may form on the sides of the carinae, either individually or in short series. In the latter case, secondary carinae form between the

Fig. 135 ▲

Figs. 135, 136 *Pachyseris rugosa* from Butterfly Bay, Hook Island, Whitsunday Islands.

Fig. 136 ▼

axial and non-axial series and these give rise to further series which develop into a sub-branch. Thus, coralla with complex branching patterns have very irregular carinae which are usually short, even monticule-like.

The appearance of the septo-costae varies greatly according to the shape of the carinae (and consequently the growth form). They are always very evenly exsert and regularly spaced and are continuous across the width of the carinae. They are perpendicular to the corallum surface or are inclined obliquely or curved. At the base of most coralla the low, wide septo-costae are relatively thick and usually two alternating orders can be distinguished. Higher on the branches where the carinae are more acute, they are usually thin and equal, always with evenly granulated sides and usually with very fine margins. Their inner margins are near vertical and are frequently anastomosed to form a discontinuous, very fine plate lining the deep central groove. The columellae are always conspicuous. They consist of fine, vertical, continuous or subcontinuous plates secondarily thickened by minute horizontal dissepiments frequently giving the upper margin a tri-ridged appearance. Sometimes the horizontal dissepiments reach the septal margins forming a shallow floor to the central groove.

Colonies are evenly coloured, usually blue-grey. Polyps are frequently expanded during the day.

Skeletal variation

The range of nominal species of *P. rugosa* reflects the wide variation observed in almost all its skeletal components. Large colonies usually consist of masses of anastomosing branches of very irregular shape. The more irregular the branches the more irregular the carinae and, in turn, the more irregular the corallites, both in position and structure. Conversely, coralla forming flat plates have regular rows of carinae with uniform, axial corallites. Thus, the skeletal characteristics of the

Fig. 137 *Pachyseris rugosa* from Cateran Bay, Border Island, same corallum as Fig. 132 (× 4.0).

corallites are strongly correlated with the growth form. Some coralla of the present series, which are composed of unifacial laminae as well as highly contorted branches, exhibit the full range of skeletal characters described above. These include septa which clearly alternate at the base, but which are equal on the branches, and totally axial calices at the base but which are both axial and non-axial on the branches.

As with some other species (e.g. *Hydnophora exesa*), the various growth forms of *P. rugosa* do not form distinctive ecomorphs. The species favours protected waters where very large colonies form; these usually display the full range of variation of the species.

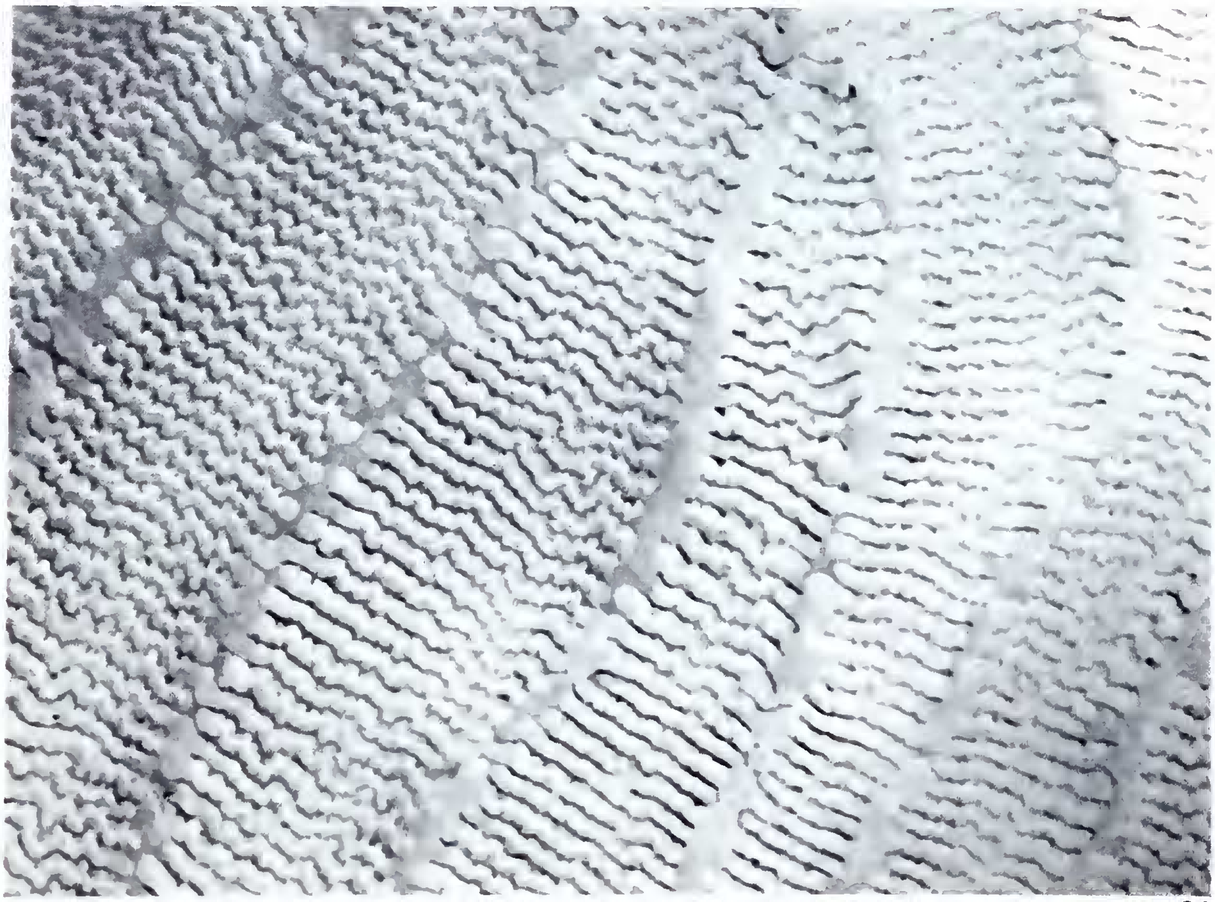
Affinities

The two species of *Pachyseris* from the Great Barrier Reef are easily distinguished on the basis of growth form which is always laminar in *P. speciosa* and by the columella which is always well formed in *P. rugosa* and absent or rudimentary in *P. speciosa* (compare Figs. 137, 138). The genus *Pachyseris*, although very discrete, has clear affinities with other Agariciidae especially *Gardineroseris* and *Pavona*. Septal characteristics of all three are very similar and the mode of formation of secondary carinae in *Pachyseris* is similar to that of *Gardineroseris*.

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea to the Caroline and Marshall Islands and Samoa.

Fig. 138 *Pachyseris speciosa* from Orpheus Island, Palm Islands, collecting station 91 (× 9.0).



Pachyseris speciosa (Dana, 1846)

Synonymy

Agaricia speciosa Dana, 1846.

Pachyseris speciosa (Dana); Edwards & Hamie (1851a, 1860); Studer (1880); Duncan (1884); Quelch (1886); Ortmann (1888); Vaughan (1918); van der Horst (1921); Matthai (1924, 1948a); Hoffmeister (1925); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Crossland (1952); Wells (1954); Nemenzo (1955a); Searle (1956); Ma (1959); Pichon (1964); Chevalier (1968); Scheer (1972); Scheer & Pillai (1974).

Pachyseris haimei Quelch, 1886.

Pachyseris clementei Nemenzo, 1955a.

Quelch considered the *P. speciosa* of Edwards & Haime to be different from Dana's and proposed the name *P. haimei* for it. The two species are discussed at length by van der Horst who considered them synonymous.

Pachyseris clementei also appears to belong to this species as it is only differentiated by the presence of a 'vesicular' lower surface which is 'not very extensive', on one of the two specimens so named by Nemenzo. It is noted, however, that no specimens of the present series have this character.

Material studied

Bramble Cay (2 specimens), **Black Rocks, Darnley Island** (2 specimens), **Big Mary Reef** (2 specimens), **Yorke Island, Warrior Island** (5 specimens), **Dungeness Island** (2 specimens), **Turtle Backed Island, Murray Islands, Bewick Island, Lizard Island** (2 specimens), **Yonge Reef, Hope Island** (2 specimens), **Low Isles** (2 specimens), **Palm Islands** (33 specimens), **Swain Reefs** (2 specimens).

These localities include collecting stations 3, 12, 13, 18, 28, 32, 34, 36, 37, 38, 41, 42, 43, 45, 55, 57, 58, 60, 68, 79, 91, 92, 93, 121, 122, 123, 127, 128, 131, 138.

Previous records from Eastern Australia

Murray Islands, Vaughan (1918); **Low Isles,** Yonge (1930), Crossland (1952).

Characters

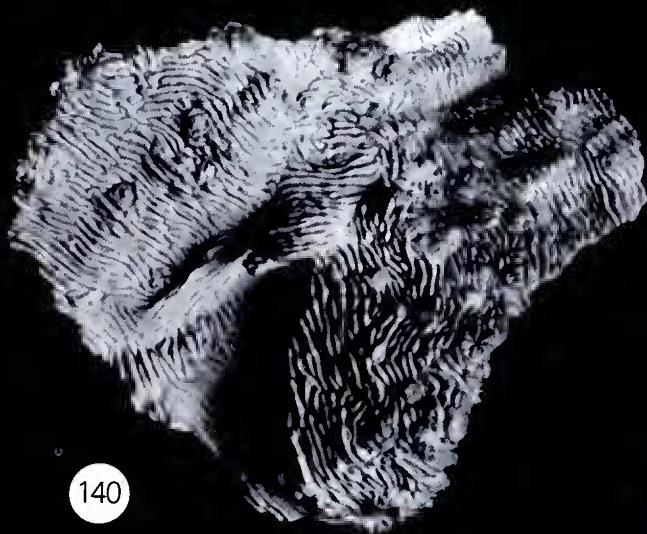
Coralla are encrusting or laminar (Fig. 748), usually forming irregular sheets, rarely contorted into hollow folds or columns (Figs. 139-142). Laminae are usually thin and delicate and are unifacial except where laminae are folded back to back.

Calices or valleys are arranged in approximately concentric rows separated by carinae which are 2-8 mm wide. The carinae may be wide and flat or acute or have one side vertical or even undercut. The calices are minute and are spaced at intervals of 1 mm along a well defined groove. In coralla with symmetrical carinae, this groove is centred along the valley axis, otherwise the groove is closer to the sides of the carinae which are steepest. In many coralla with carinae having a vertical or undercut side, there may be two rows of calices, one at the bottom of this side and a secondary row higher on the opposite slope. The secondary row is usually short with relatively well defined centres. Sometimes they are monocentric. Secondary carinae sometimes form between the two rows (as described for *P. rugosa*) which may develop into small protuberances.

Figs. 139-142 *Pachyseris speciosa* (× 0.5).

Fig. 139 From the Swain Reefs, collecting station 79.
Fig. 140 From Bullumbooroo Bay, Great Palm Island.
Fig. 141 From Darnley Island, collecting station 31.
Fig. 142 From Orpheus Island, Palm Islands, collecting station 91.


139


140


141


142

Septo-costae are similar to those of *P. rugosa* except that in some coralla they may be wavy or even crenellated. Two alternating orders can be distinguished in some coralla, in others they are exactly equal. They are frequently tri-ridged and are always granulated. The calicular groove consists of flattened septal margins (frequently only those of the first order) and horizontal dissepiments. The position of individual calices is often very indistinct. Columellae are not developed or, rarely, are very rudimentary. The under surfaces of coralla are finely costate, usually ornamented with minute spines.

Living colonies have mostly uniform colours, usually dark or pale grey or brown.

Growth form variation

This species is frequently found in environments of low light intensity where coralla largely consist of very thin, sometimes overlapping laminae with low carinae and regular axial grooves. Coralla from more exposed biotopes usually develop high, asymmetrical carinae, as described above, and form thicker laminae. Otherwise there is very little variation within the species.

Affinities

This species resembles *P. rugosa* but is always distinguished by its laminar growth form and lack of well defined columellae.

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea to the Marshall Islands, Samoa and Tahiti.

Fig. 143 *Pachyseris speciosa* from the Palm Islands.

IV
Family Siderastreidae Vaughan & Wells, 1943

The Siderastreidae are a small family composed of only five recent genera, one of which, *Siderastrea,* occurs in both the Atlantic and in the Red Sea-Indian Ocean. The Siderastreidae are particularly well represented in the Western Indian Ocean where 4 genera can frequently be recorded in any one locality.

The siderastreids are essentially characterised by the septothecal structure of the wall, the tendency for the inner margins of septa to unite forming groups of confluent septa and the strongly granulated nature of the septal margins and sides.

Vaughan & Wells (1943) noted the similarities in the septal structures of the Siderastreidae and Thamnasteriidae and the close affinities between these two families (particularly between *Coscinaraea* and *Psammocora*) have already been discussed by the authors (1976, p. 21).

Two genera are present in eastern Australia, *Coscinaraea* and *Pseudosiderastrea* and both may be abundant in some biotopes. The remaining three genera of the family, *Siderastrea, Anomastraea* and *Horastrea,* are restricted to the Red Sea and/or western Indian Ocean.

GENUS *PSEUDOSIDERASTREA* YABE & SUGIYAMA, 1935

Introduction

Pseudosiderastrea was created by Yabe & Sugiyama (1935) for *P. tayamai,* a new species from the Arafura Sea having affinities with two other Siderastreidae, *Anomastraea* and (especially) *Siderastrea.* Vaughan and Wells (1943) and Wells (1956) treated *Pseudosiderastrea* as a subgenus of *Anomastraea.*

Large collections of *Siderastrea radians, Anomastraea irregularis* and *Pseudosiderastrea tayamai* were re-examined during the present study which supports the Japanese authors' conclusion that *Pseudosiderastrea* is closer to *Siderastrea* than *Anomastraea.*

Although the wall structures of *Anomastraea* and *Pseudosiderastrea* are similar in usually having one row of synapticulae, the latter has the same extratentacular budding as *Siderastrea* of which it can be considered as a very cerioid form.

Pseudosiderastrea tayamai Yabe & Sugiyama, 1935

Synonymy

Pseudosiderastrea tayamai Yabe & Sugiyama, 1935; Yabe, Sugiyama & Eguchi (1936); Searle (1956).

Anomastraea (*Pseudosiderastrea*) *tayamai* (Yabe & Sugiyama);Vaughan & Wells (1943); Wells (1956).

Figs. 144-147 *Pseudosiderastrea tayamai* (× 5.0).

Fig. 144 From Magnetic Island.
Fig. 145 From Pelorus Island, Palm Islands, collecting station 90 showing confluent septa and intramural synapticular ring.
Fig. 146 From the Palm Islands, showing extratentacular budding.
Fig. 147 From Pioneer Bay, Orpheus Island, collecting station 45, showing septal dentations.

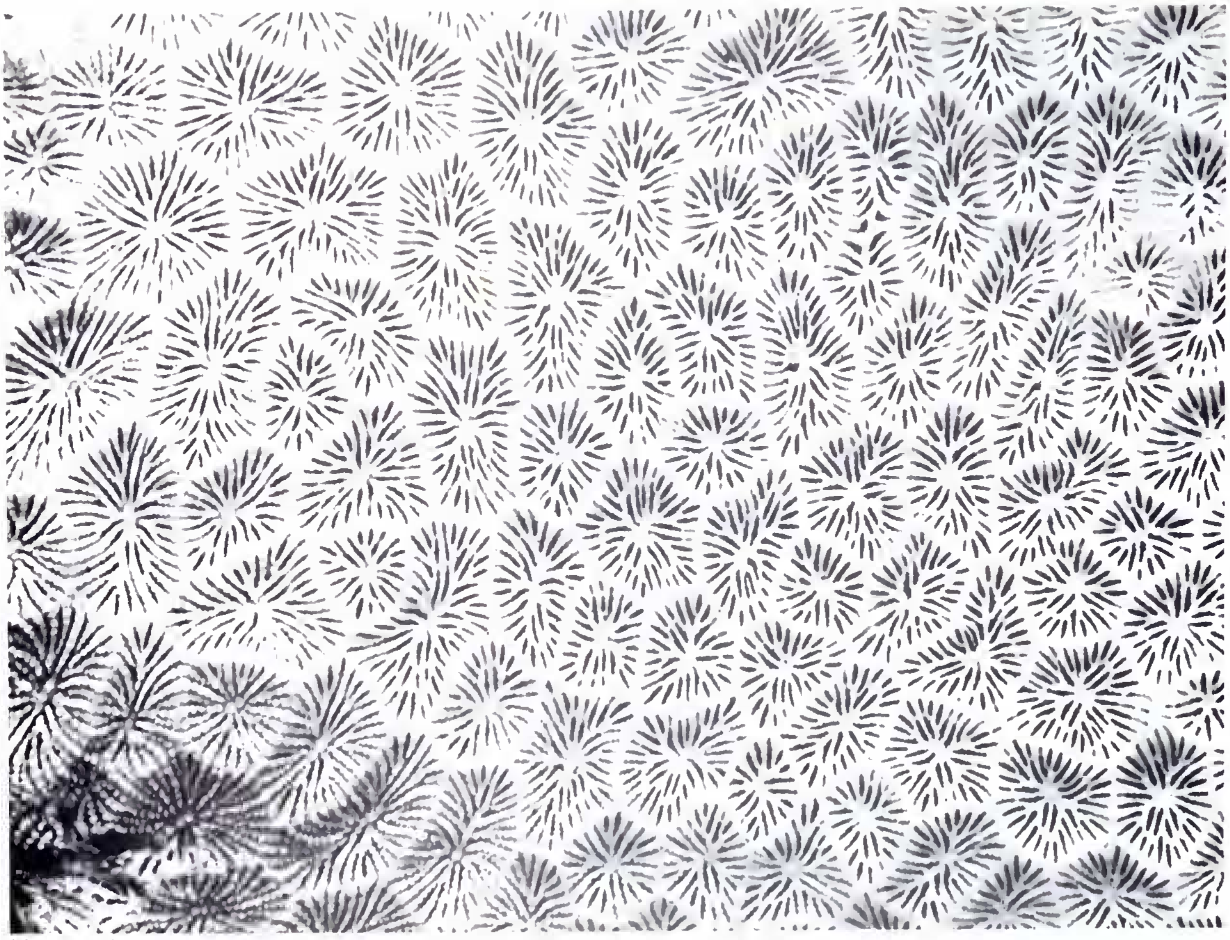
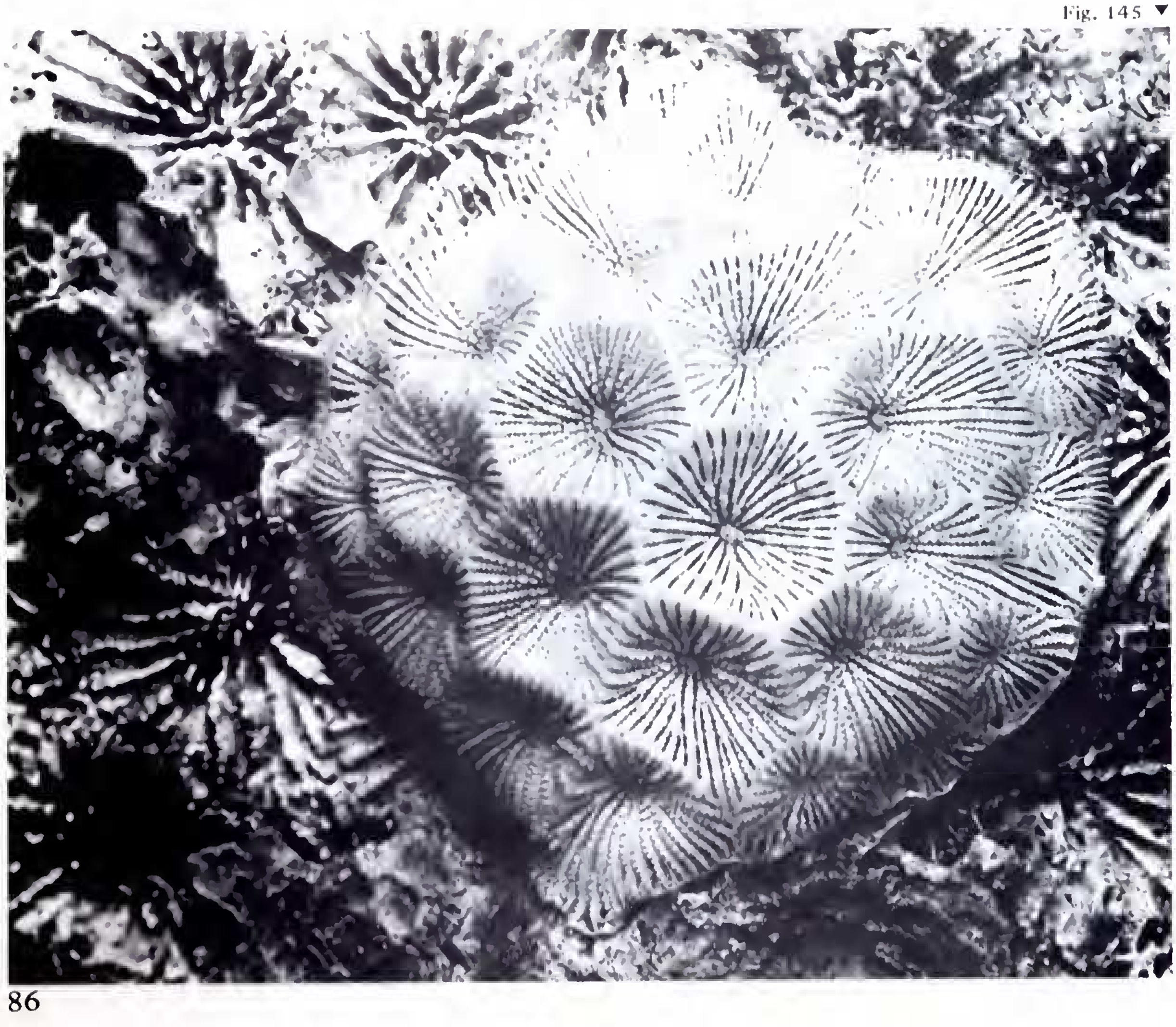


Fig. 144 ▲

Fig. 145 ▼



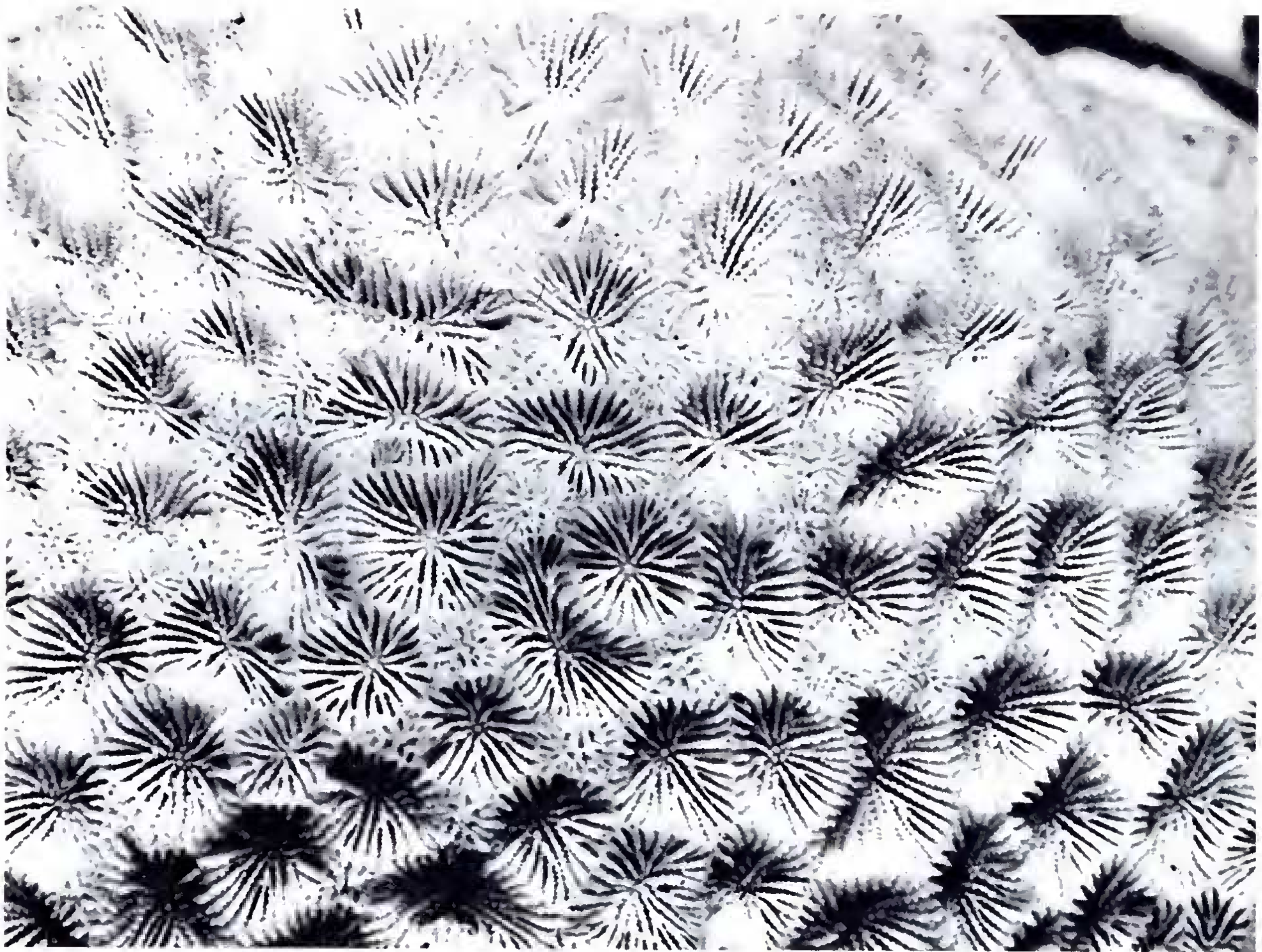
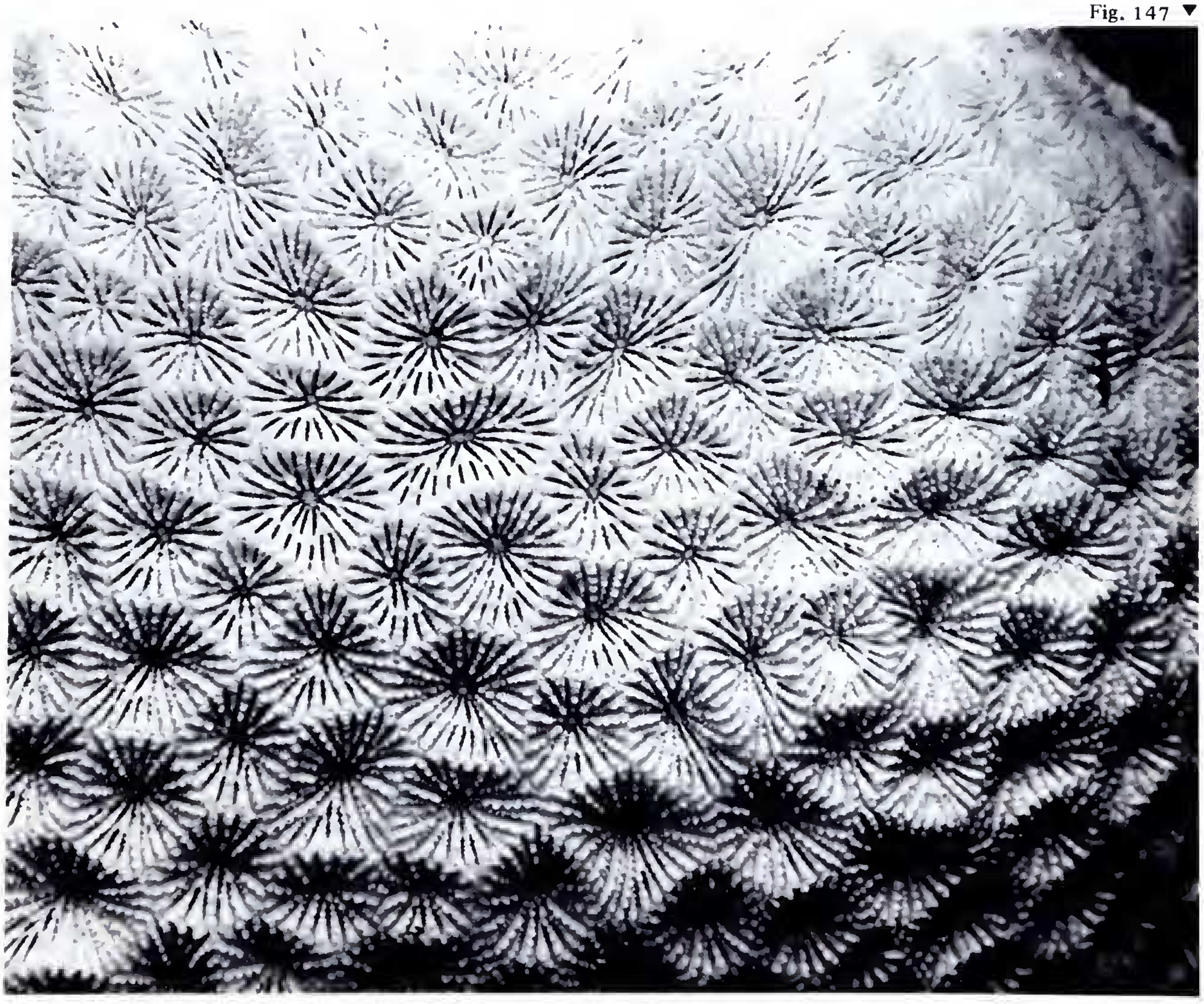


Fig. 146 ▲

Fig. 147 ▼



Anomastraea irregularis (von Marenzeller); *sensu* Crossland, 1952.

Siderastraea savignyana (Edwards & Haime); *sensu* van der Horst, 1921.

Material studied

Warrior Reef, Thursday Island (2 specimens), **Lizard Island, Eagle Reef, Plug Reef, Palm Islands** (5 specimens), **Keeper Reef, Magnetic Island** (27 specimens), **Whitsunday Island** (3 specimens).

These localities include collecting stations 45, 53, 54, 59, 64, 90, 97, 98.

Previous records from Eastern Australia

Torres Strait, Clarke Island, Wells (1955a); **Low Isles** (as *Anomastraea irregularis*) Crossland (1952); **Cape Cleveland, Port Newry, Redbill Reef, Northumberland Islands,** Wells (1955a).

Characters

Coralla are thick encrusting, sometimes massive, up to 16 cm maximum diameter. Corallites are generally polygonal, shallow, 3-6 mm diameter, sometimes elongated in the flat or concave parts of the corallum. Up to 48 septa are arranged in four cycles, the fourth cycle being incomplete. Septa of the higher cycles tend to fuse by their inner margin to septa of lower cycles forming groups of septa commonly found in the Siderastreidae. Septa are slightly exsert. Their upper and inner margins are gently and regularly inclined toward a conspicuous axial fossa 0.4-0.5 mm in diameter. Their margins bear small but well defined, equal or subequal dentations or granules flattened perpendicularly to the septa. There are 10 to 12 dentations or granules on the primary septa. Septa are compact; their sides are covered with small spines, often arranged in rows of trabecular direction. There are one or two incomplete, irregular, synapticular rings. The corallite wall is synapticulothecal, thin but solid and always clearly distinct. Columellae are composed of 1-4 low, rounded bosses or papillae, which are the upward extremities of a few trabeculae projecting above the floor of the fossa. Budding is extratentacular, similar to that of *Siderastrea.*

Living colonies are pale grey or pink in colour with white corallite walls (Fig. 749).

Skeletal variation

Pseudosiderastrea tayamai shows little intraspecific variability. Minor variation may occur in the regularity and depth of the corallites, which is mostly a function of age, and slight variation occurs in the thickness of the corallite wall and in the thickness and number of septa.

Affinities

Van der Horst's (1922a) record of *Siderastraea savignyana* from Aru Island was a misidentification of *P. tayamai.* Likewise Crossland's (1952) *Anomastraea irregularis* from Low Isles, is a small but typical *P. tayamai.*

The only conservative character that *Anomastraea* and *Pseudosiderastrea* have in common is a thin wall, usually composed of only one row of synapticulae. Apart from having different budding characteristics, the corallites of *Anomastraea* are deeper, their central fossa is wider, the septa are comparatively narrow and a different shape, being horizontal at the perimeter then falling abruptly to the corallite floor.

Siderastraea savignyana and *P. tayamai* are primarily distinguished by the characters of the corallite wall. Otherwise they are similar, especially when the former has shallow corallites.

Distribution

Recorded from south India, Madagascar, Singapore, the Philippines, the Celebes and the Great Barrier Reef.

GENUS *COSCINARAEA* EDWARDS & HAIME, 1848

Generic synonymy

Coscinastrea Edwards & Haime, 1848c. (Edwards & Haime, 1860 noted that this spelling was a printing error).

Type species *Coscinaraea monile* (Forskål, 1775) = *Coscinaraea bottae* Edwards & Haime, 1848.

Characters of the genus (partly after Wells, 1956)

Coralla are massive, subspherical, columniform or encrusting. Colony formation is by intratentacular, mono- to poly-stomodaeal budding and coralla are cerioid to meandroid. The wall is synapticulothecal, composed of several rings of synapticulae forming low collines. Septa are perforate, composed mostly of compound synapticulae.

Introduction

About 14 nominal species of *Coscinaraea* have been referred to in the literature, and a new species is described below. Of these, perhaps only 7 are valid species: *C. monile, C. columna, C. exesa, C. wellsi, C. mcneilli, C. marshae* and *C. crassa*. The status of *C. ostreaeformis* remains doubtful. Three of these species, *C. mcneilli, C. marshae* and *C. crassa* are known only from Australia, the two former being restricted to temperate waters, *C. mcneilli* from SE and S Australia and *C. marshae* from W Australia, between Fremantle and Geographe Bay. Only *C. monile*, from the Red Sea and Indian Ocean, has not been recorded from Australia.

Gardiner (1905) noted the undeniable relationships between *Coscinaraea* and *Psammocora*, as exemplified, by *C. exesa*. The distinction between the two genera is essentially based on the existence of compound trabeculae, and of a true synapticulothecal wall in *Coscinaraea*.

Coscinaraea exesa (Dana, 1846)

Synonymy

Psammocora exesa Dana, 1846; *non* Edwards & Haime (1860); Brüggemann (1879b); Quelch (1886); Rehberg (1892); Gardiner (1905); van der Horst (1921, 1922a); Yabe & Sugiyama (1935a); Yabe, Sugiyama & Eguchi (1936); Crossland (1952); Nemenzo (1955).

Material studied

Bushy Island-Redbill Reef (4 specimens), **Swain Reefs** (4 specimens), **Heron Island.**

These localities include collecting stations 67, 68, 73, 76, 79, 116.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are columnar, sometimes claviform or digitate with a flat top. Corallites are superficial at the base of the colony, or at the base of the columns. They are up to 6 mm diameter with 18-24 septa at the periphery of which approximately 8 reach the central fossa. Septa have fused inner and (sometimes) outer margins, with

enclosed septa having a petaloid shape. Septa are granulated, except for those on the tops of columns, with granulations sometimes developing into distinct lobes. They are thinner and less compact than at the base of the corallum where the petaloid appearance tends to disappear. Towards the tip of columns, collines are better developed and wider, but remain irregular, enclosing one or a short series of corallites. They may develop independently of the serial arrangement of corallites, as they do in *Psammocora superficialis*. On horizontal parts of coralla, corallites are separated by an extensive, very porous, echinulate coenosteum. Columellae are composed of rounded, upward projecting (papillary) trabeculae.

Affinities

Ever since its original description as *Psammocora exesa*, this species has been confused with *Coscinaraea columna* and especially with *Psammocora digitata* Edwards & Haime, a senior synonym of *Psammocora togianensis* Umbgrove (see Veron & Pichon, 1975, p. 30). Both *Coscinaraea exesa* and *Psammocora digitata* have a similar general growth form with more or less cylindrical vertical columns, and both have petaloid septa although this is less conspicuous in *C. exesa*.

However, the generic position of *C. exesa* is clear; its trabeculae, synapticular walls and columellae with papillary trabeculae are clearly *Coscinaraea*-like. Within *Coscinaraea*, *C. exesa* is closest to *C. columna* (as previously noted by Wells, 1954, p. 410). It differs in having consistently superficial, larger corallites with less numerous, thicker septa and almost always has a columnar growth form.

Distribution

Known only from the Great Barrier Reef and Fiji.

Fig. 148 *Coscinaraea exesa* from Bushy Island, collecting station 73, showing the typical columnar growth form (× 0.5).

Fig. 148 ▼

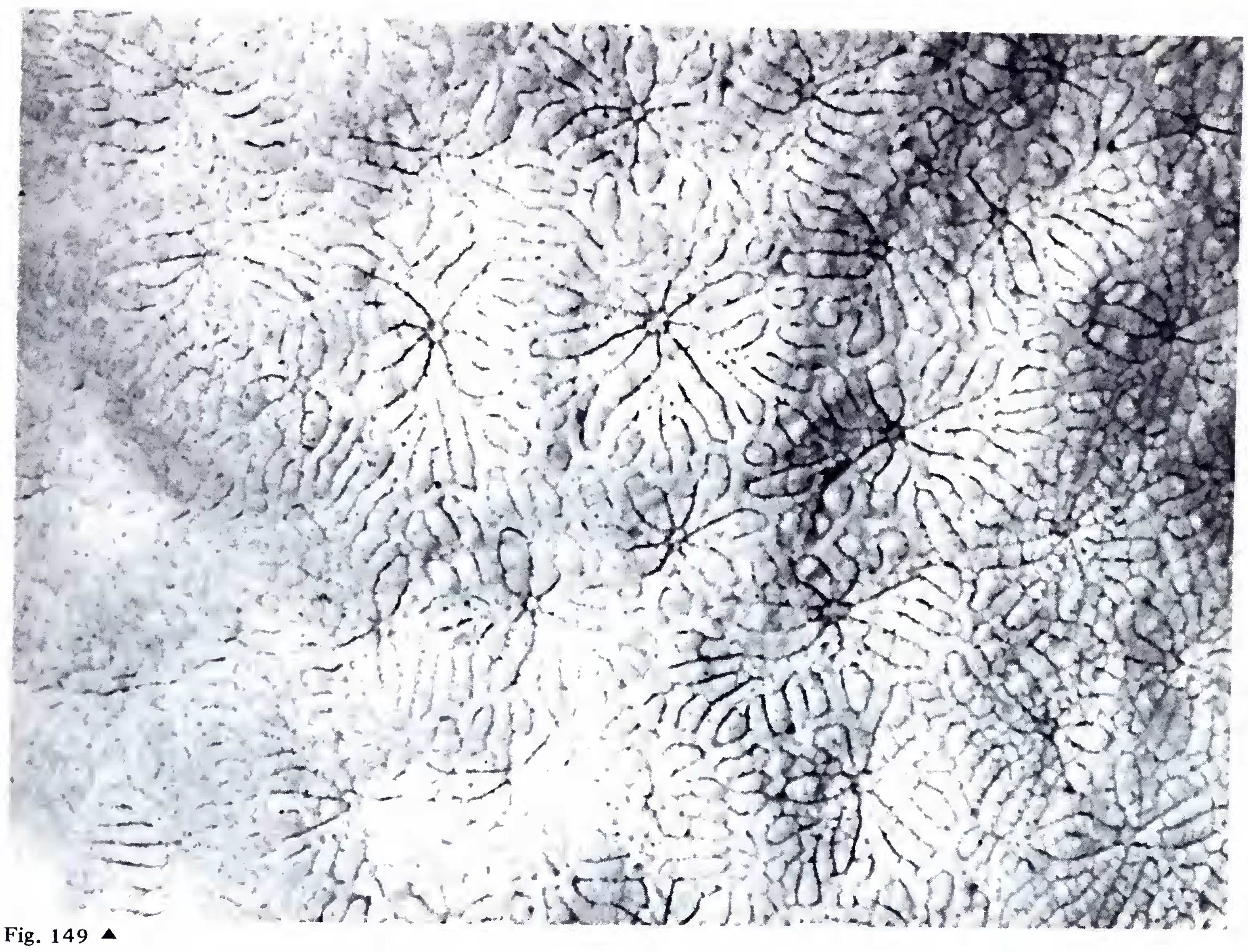
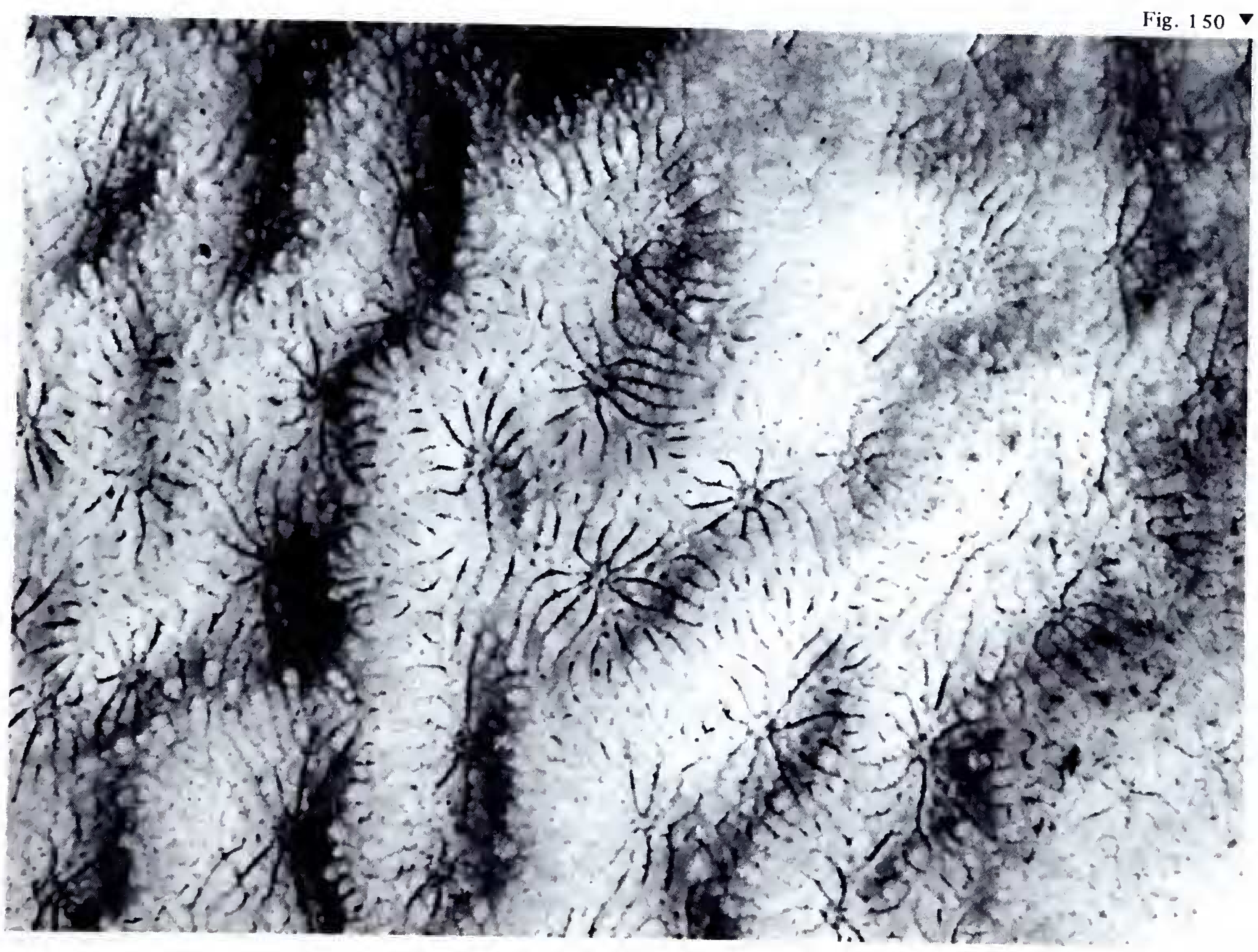


Fig. 149 ▲

Figs. 149, 150 *Coscinaraea exesa* same corallum from Bushy Island, collecting station 73 (× 5.0).

Fig. 150 ▼



Coscinaraea columna (Dana, 1846)

Synonymy

Psammocora columna Dana, 1846; Matthai (1923a).

Psammocora fossata Dana, 1846; Whitelegge (1898); Ma (1959).

Psammocora savigniensis Gardiner, 1898.

Coscinaraea columna (Dana); Hoffmeister (1925); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Wells (1954, 1955b); Nemenzo (1955a); Stephenson & Wells (1955); Pichon (1964).

Coscinaraea fossata (Dana); Hoffmeister (1925); Umbgrove (1940); Wells (1954).

Coscinaraea kusimotoensis Yabe, Sugiyama & Eguchi, 1936.

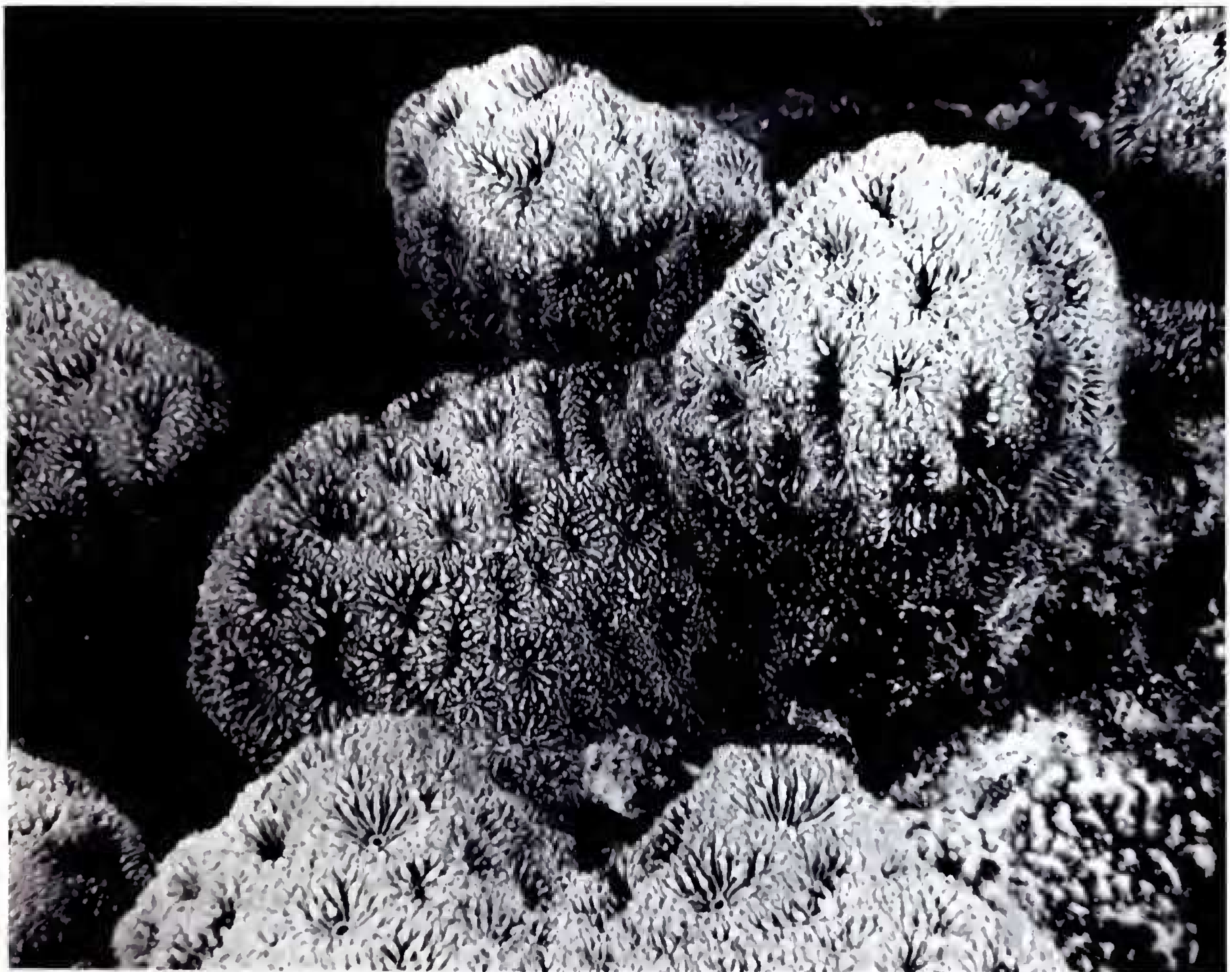
Coscinaraea hahazimaensis Yabe, Sugiyama & Eguchi, 1936; Ma (1959).

Material studied

Reef NE of **Murray Islands, Murray Islands** (8 specimens), **Yorke Island** (3 specimens), **Great Detached Reef** (5 specimens), **Tijou Reef, Jewell Reef, Lizard Island** (2 specimens), **Yonge Reef** (2 specimens), **MacGillivray Reef, Ribbon Reef, Feather Reef, Nathan Reef, Sandy Cay, Bowl Reef** (3 specimens), **Lodestone Reef, Palm Islands** (8 specimens), **Whitsunday Islands, Bushy Island-Redbill Reef** (3 specimens), **Pompey Complex** (2 specimens), **Swain Reef** (8 specimens), **Lord Howe Island** (6 specimens).

These localities include collecting stations 1, 5, 8, 9, 10, 27, 28, 30, 32, 34, 35, 36, 42, 58, 63, 67, 68, 69, 71, 73, 74, 76, 77, 80, 96, 99, 103.

Fig. 151 *Coscinaraea exesa* from the Swain Reefs, showing *in situ* appearance.



Previous records from Eastern Australia

Low Isles, Stephenson & Wells (1955); **Heron Island** (as *C. monile*), Salter 1954; **Solitary Islands,** Veron *et al.* (1974); **Lord Howe Island,** Veron (1974), Veron & Done (1979).

Characters

Coralla are thin, encrusting or explanate to massive and columniform. Corallites are single or are arranged in series circumscribed by collines of variable height and shape. They are usually 3 to 4 mm diameter, with extreme values of 1.5 to 6 mm. Up to 40 septa occur at the periphery which are rapidly reduced by fusion to 12-15 at the central fossa.

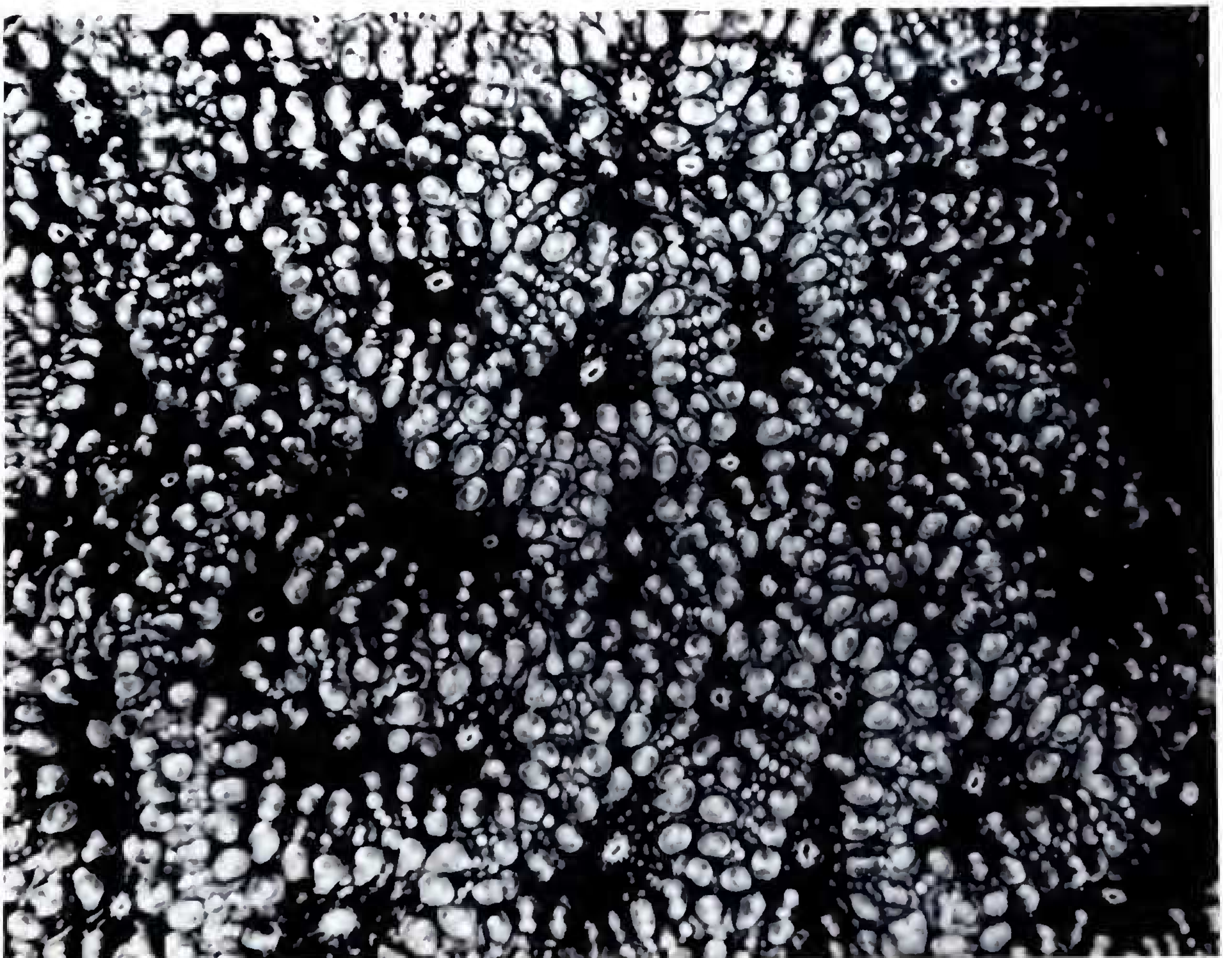
Septal margins bear numerous hirsute granules which are the tips of compound trabeculae. They are perforate, with granulated sides. The wall is synapticulothecal and well defined. Columellae are conspicuous, composed of one or several upward projecting papillae.

Living colonies (Fig. 751) are brown to purple in colour.

Skeletal variation

As mentioned by Wells (1954), *C. columna* shows wide variation, notably in the size and shape of the collines, the size of valleys and in corallite structures. Collines may be well developed, up to 4 mm high or almost totally lacking, giving the corallum an even appearance with superficial corallites. This tends to occur at the perimeter of most coralla irrespective of growth form. Collines also vary in shape, from very rounded to subacute, with consequent formation of narrow to open valleys, with flat

Fig. 152 *Coscinaraea columna* from Lord Howe Island, showing polyps with tentacles retracted.



floors. Valleys vary in length from that of single corallites to series up to 5 cm long including up to 12 centres. The number and width of septa and consequently the width of the interseptal loculi also vary.

Affinities

The affinities of *Coscinaraea* species have been discussed by Hoffmeister (1925), Umbgrove (1940) and Wells (1954, 1962). Both Hoffmeister and Umbgrove considered *C. fossata* a synonym of *C. monile*, while Wells (1954) separated them, and the former, from *C. columna*.

The present study indicates that *C. monile* is a separate species from *C. fossata* and that *C. meandrina* is a synonym of it. *Coscinaraea fossata* and *C. columna* are the same species (the resemblance was mentioned by Dana himself), and the latter name is chosen for it. Synonyms of *C. columna* clearly include *C. savigniensis, C. hahazimaensis* and *C. kusimotoensis*. The position of *C. ostreaeformis* van der Horst (*non* Wells, 1954) remains unsettled. It has close affinities with *C. columna*, differing mostly in the larger number of septa and the very flat appearance of the corallum. *Coscinaraea ostreaeformis* could be a deep water ecomorph of *C. columna* as the only known specimen of it was collected from >90 m depth.

Distribution

Recorded from Madagascar, the Mascarene Islands, the Great Barrier Reef, Indonesia, the Philippines, Japan, the Marshall and Ellice Islands, New Caledonia, Fiji, Samoa and the Tuamotu Archipelago.

Coscinaraea mcneilli Wells, 1962

Synonymy

Coscinaraea mcneilli Wells, 1962.

Material studied

Byron Bay (2 specimens), **St Vincent's Gulf,** South Australia (2 specimens), and specimens from the Australian Museum from **Sydney Harbour** and **Manly** (holotype and paratype).

Previous records from Eastern Australia

North Head, Sydney, Manly, Wells (1962).

Characters

Coralla are explanate, expanding horizontally in an undulating lamina, up to 2 cm thick. They are either entirely encrusting or attached to the substrate on most of the undersurface, but have free, broadly lobed, margins. They are thamnasteroid, with colony formation mostly by circumoral budding. Corallites are grouped in approximately concentric rows, 4-7 mm apart, except towards the centre of the colonies, where their distribution is irregular. Corallite rows are separated by low, wide collines with a flat upper surface. Where collines are not formed (particularly towards the corallum centre), the surface is even, with superficial corallites. Within valleys,

Figs. 153-156 *Coscinaraea columna* (× 5.0).

Fig. 153 From the Swain Reefs, collecting station 76.
Fig. 154 From Bullumbooroo Bay, Great Palm Island, collecting station 35.
Fig. 155 From Cateran Bay, Border Island, Whitsunday Islands, collecting station 96.
Fig. 156 From the Swain Reefs, collecting station 79.

Fig. 157 *Coscinaraea columna* from the Swain Reefs, same corallum as Fig. 153 (× 0.33).
Fig. 158 *Coscinaraea mcneilli* from Byron Bay, New South Wales (× 0.5).

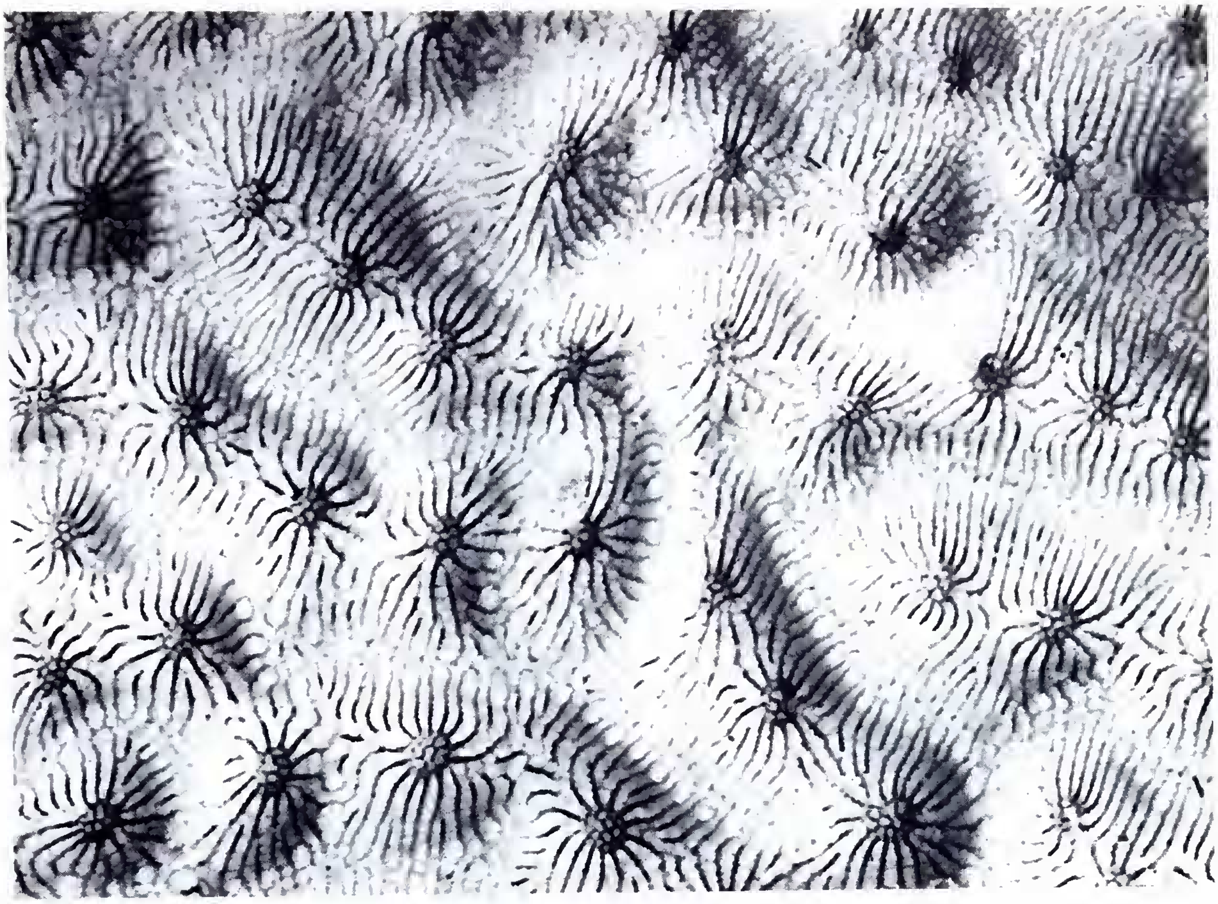
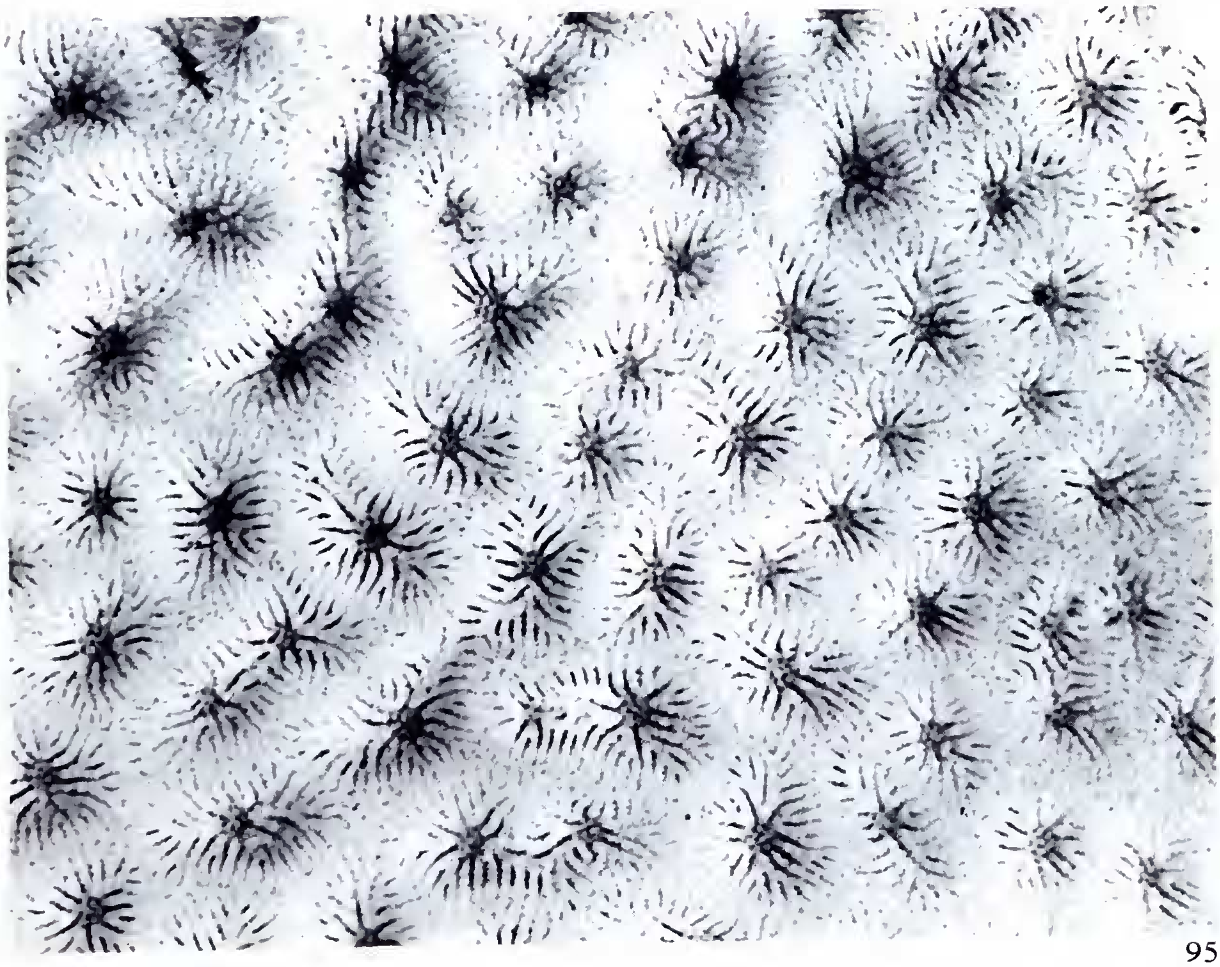


Fig.153 ▲

Fig. 154 ▼



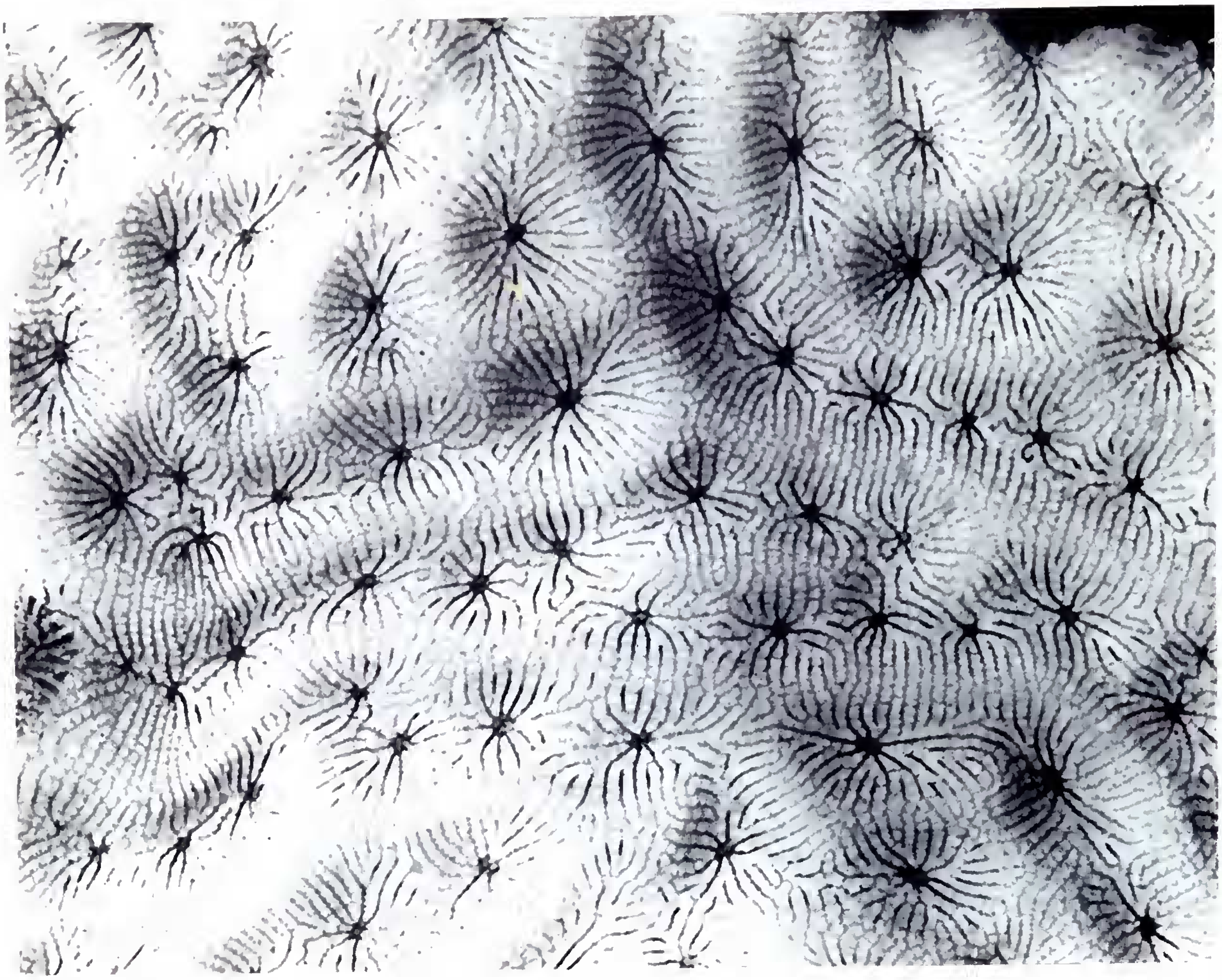
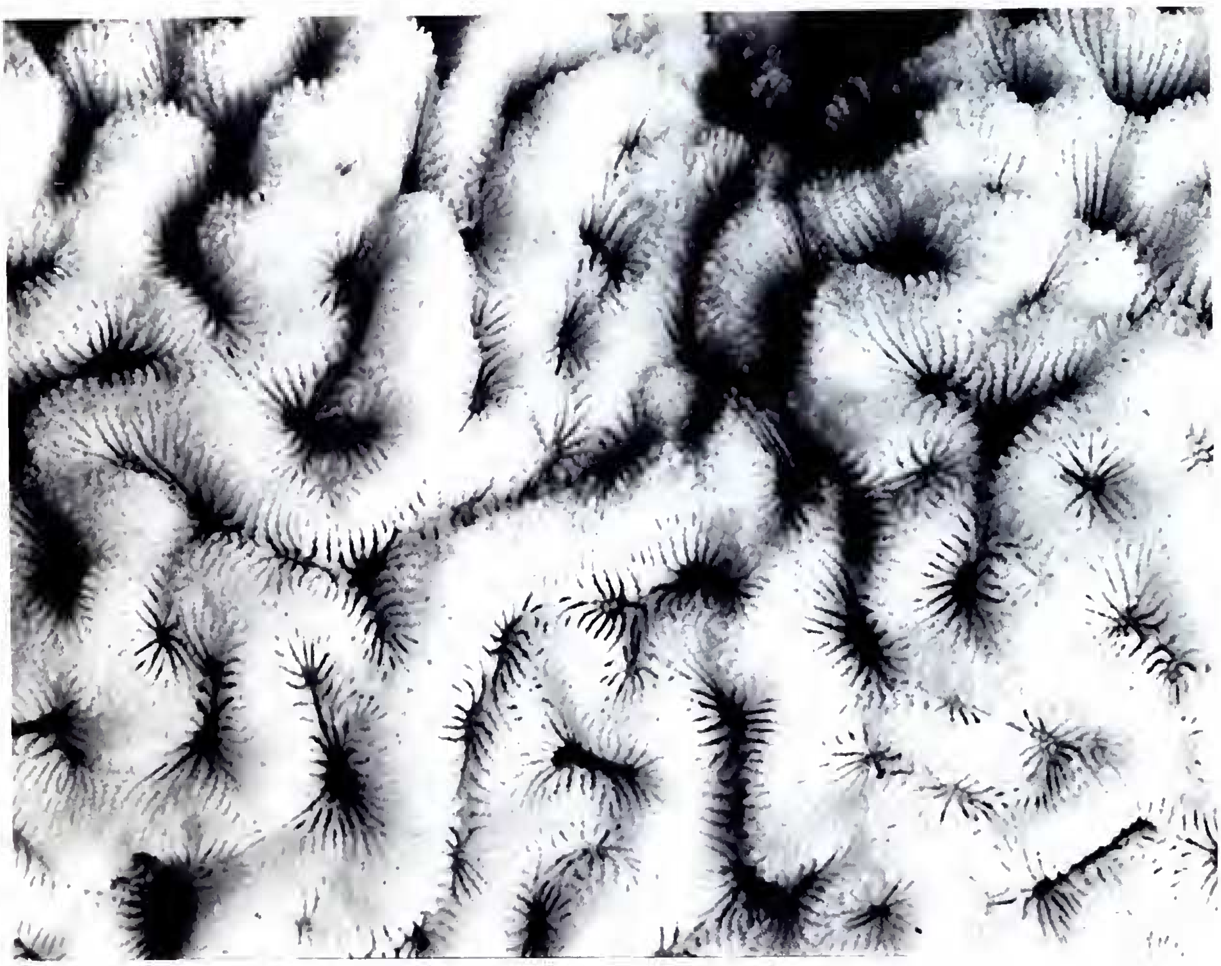


Fig. 155 ▲

Fig. 156 ▼



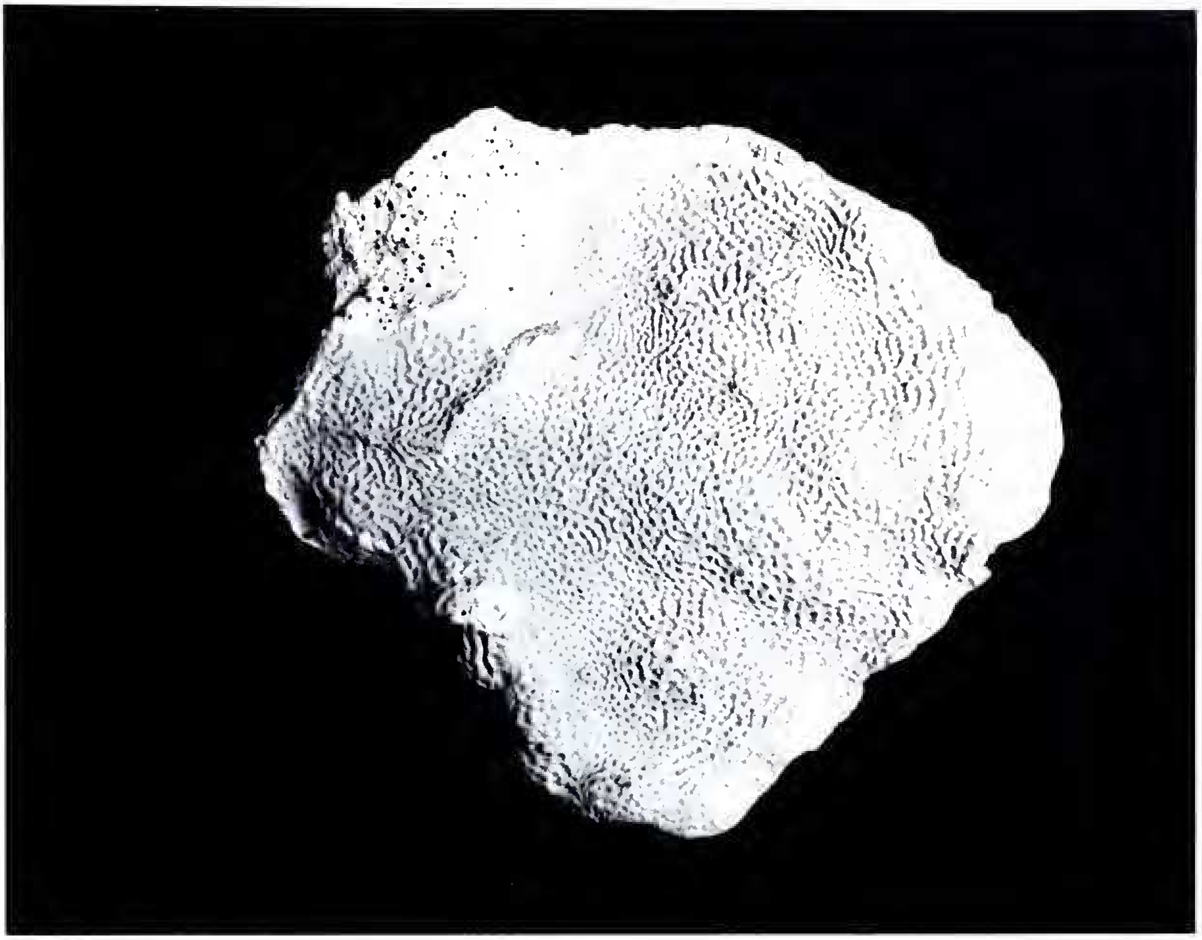
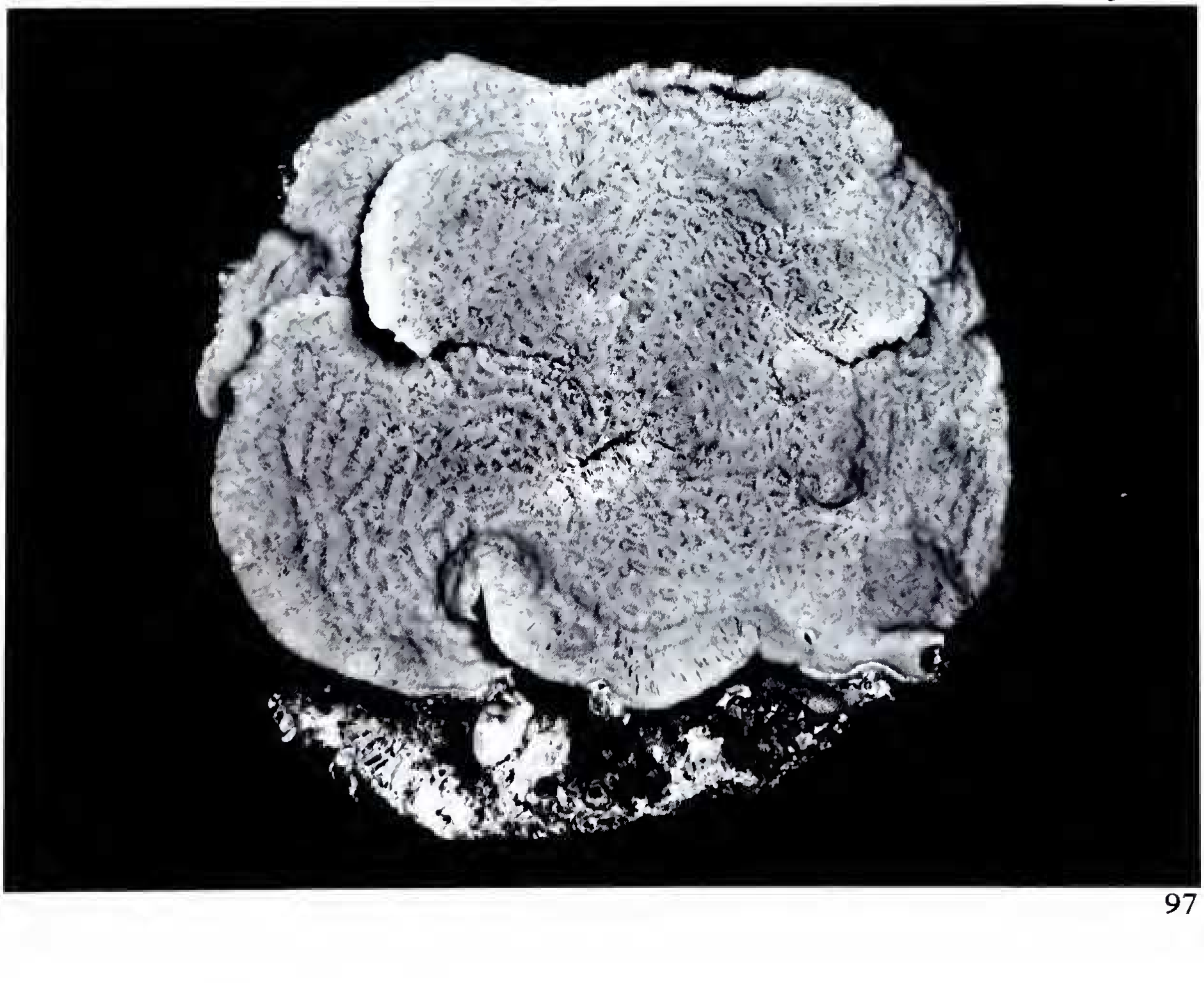


Fig. 157 ▲

Fig. 158 ▼



corallites are 2.5-6 mm apart and are connected by a solid continuous lamella or valley septum on which two opposite septo-costae fuse at right angles. Corallites have 10-40 septa, 14-20 on an average, of which 10 to 16 reach the columella. Septo-costae frequently fuse into groups towards the centre of the corallites. They are equal or subequal, getting gradually narrower towards the corallite centres. They sometimes have a zig-zag pattern, similar to that found in some species of *Leptoseris* and also in *Coscinaraea crassa*. Petaloid or subpetaloid structures (i.e. septo-costae developing a network which entirely, or almost entirely, surrounds shorter, thicker costae) are present, but uncommon. Septal margins are strongly beaded; their sides are strongly granulated. Columellae are well developed, composed of papillary trabeculae in a shallow but well defined central fossa. Corallites lack a well-defined boundary. The wall is synapticulothecal, solid and imperforate. Costa are equal and separated by narrow grooves at the corallum periphery, then become markedly unequal and regularly alternating. Towards the corallum centre the smaller costae disappear totally, leaving equal, widely spaced costae. All costae are irregularly covered with small granules.

Skeletal variation

Coscinaraea mcneilli appears to be a rare but well defined species. The few coralla of the present series display only minor variations in the ornamentation of the common wall, and in the development of the collines and columellae (better defined in specimens of the present series than in the holotype).

Distribution

Coscinaraea mcneilli appears to be restricted to south-eastern Australia (from Byron Bay to St Vincents Gulf) just as *C. marshae* Wells, 1962 appears to be restricted to south-western Australia. The only other hermatypic coral with a comparable distribution is *Scolymia australis* which may be only a south-temperate ecomorph of a tropical species (see p. 244).

Coscinaraea wellsi n. sp.

Synonymy

Coscinaraea ostreaeformis van der Horst; *sensu* Wells (1954); Maragos (1977).

Material studied

Anchor Cay, Big Mary Reef, Yorke Island (2 specimens), **Murray Islands** (3 specimens), **Lizard Island, Lord Howe Island** (4 specimens).

These localities include collecting stations 27, 125, 129, 131, 139, 143.

Previous records from Eastern Australia

Lord Howe Island, Veron & Done (1979).

Characters

Corallites are flat, encrusting to explanate lamellae with thin, lobed margins (Fig. 752). Corallites are 4 to 5 mm apart, superficial or slightly protuberant. They have 8-18 septa (averaging 10 to 14) which are equal or subequal. In the latter case, primary septa tend to develop a slightly exsert, thickened, upper lobe. Septal margins are

Figs. 159-162 *Coscinaraea mcneilli* (× 5.0).

Figs. 159, 160 From Byron Bay, Fig. 159 the same corallum as Fig. 158.
Fig. 161 From Glenelg, Victoria.
Fig. 162 From St Vincents Gulf, South Australia.

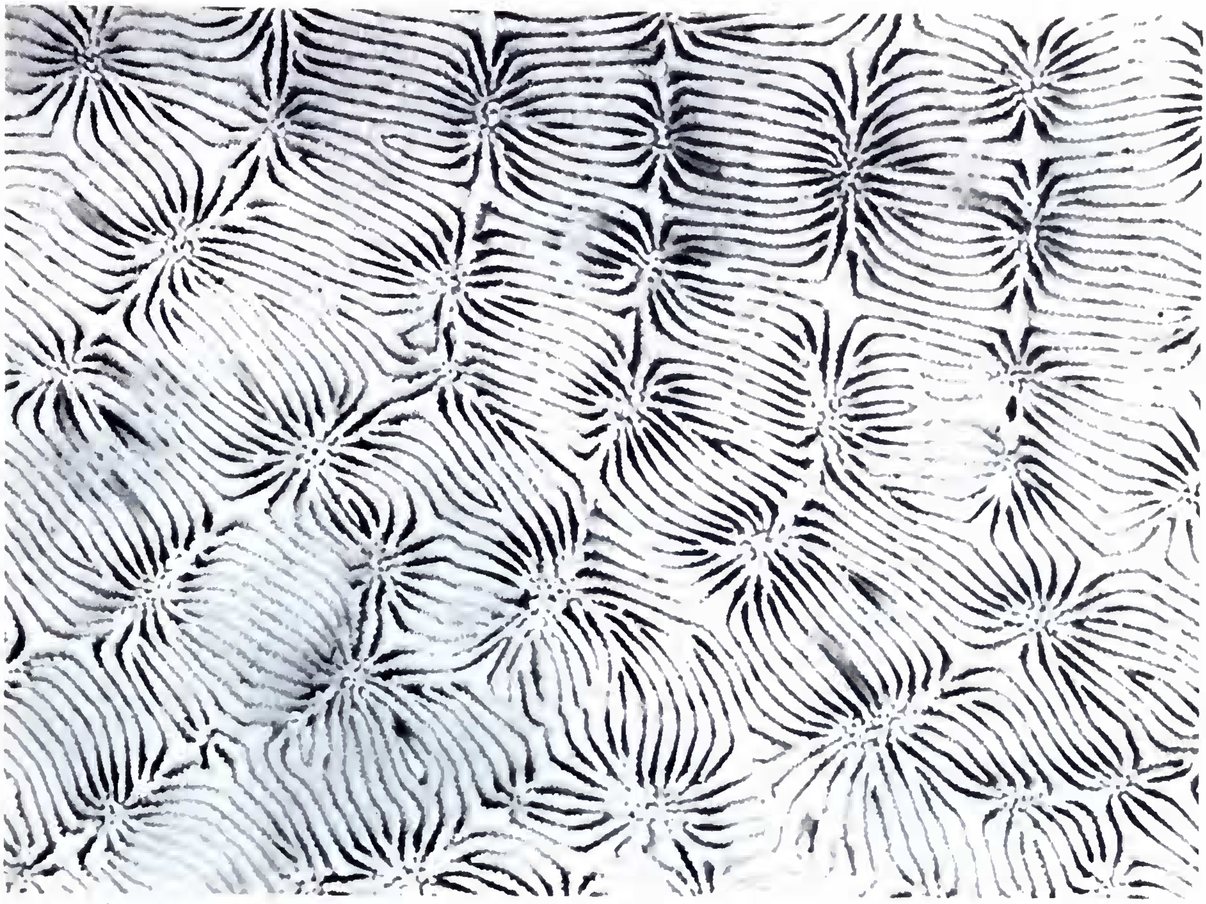
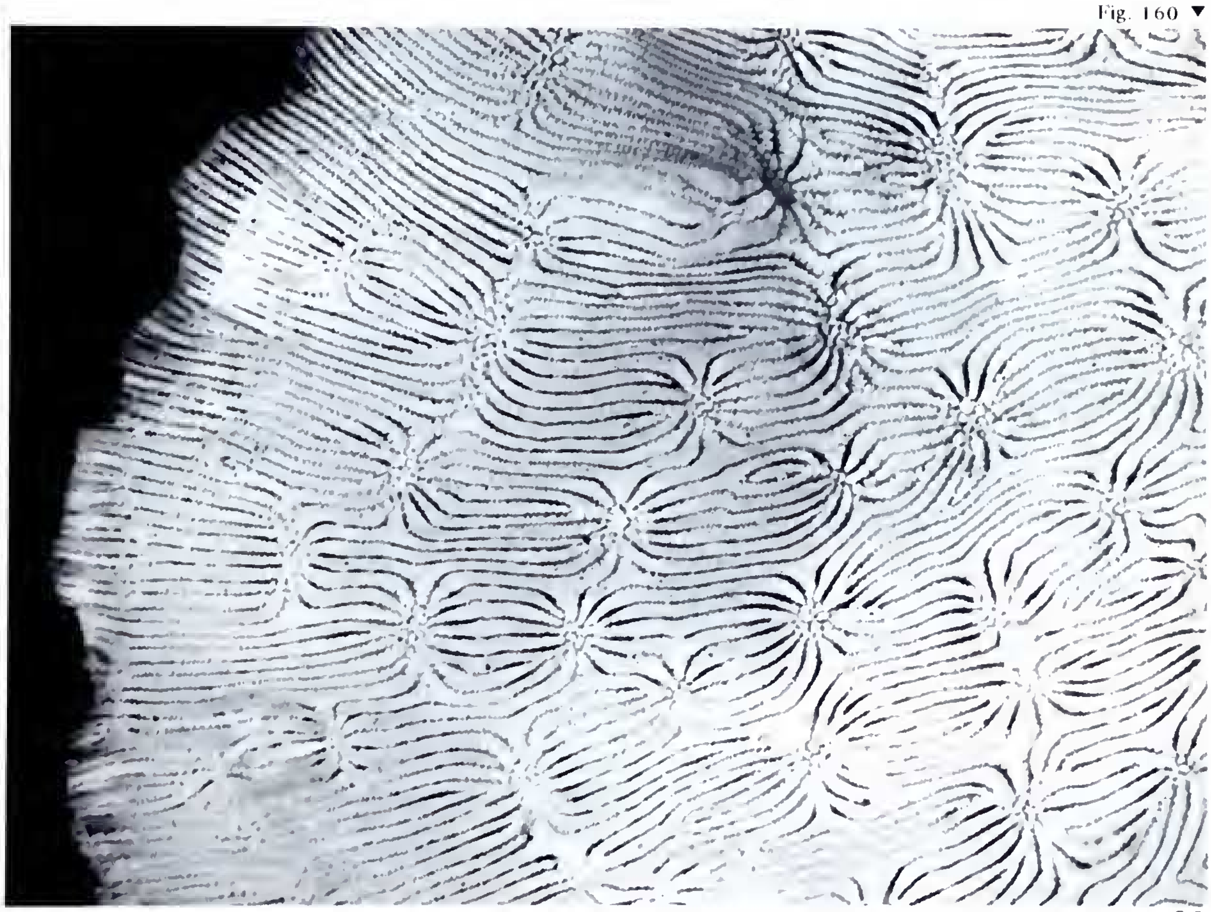


Fig. 159 ▲

Fig. 160 ▼



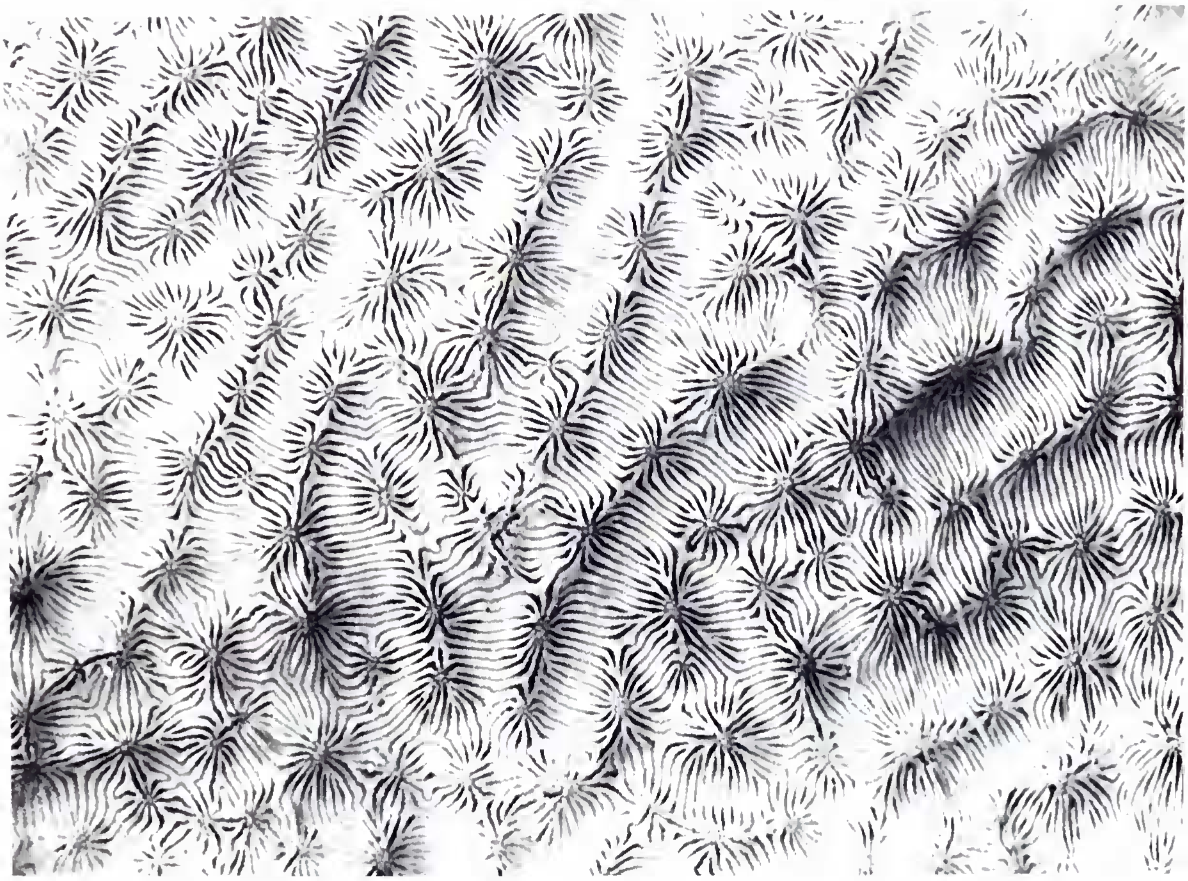
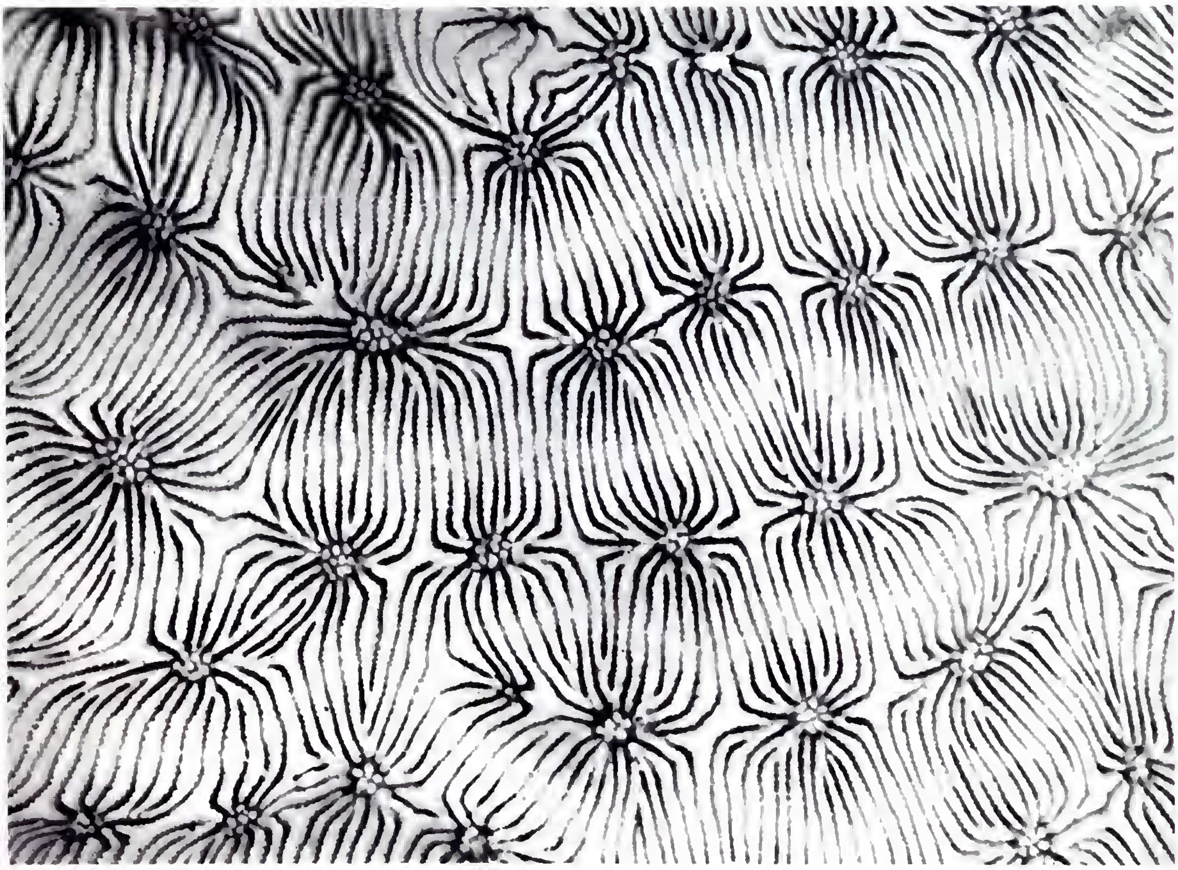


Fig. 161 ▲

Fig. 162 ▼



heavily granulated; their inner margins are vertical, limiting a well defined circular or slightly elongate central fossa, 0.5-1 mm deep. Septal sides are very granular. Septo-costae are long, usually extending from one corallite to another. There is usually a lobe, resembling a tentacle lobe, at the point of insertion of septo-costae. Two septo-costae of a higher order fuse in front of this point. Some septo-costae are thus enclosed at both ends giving a petaloid appearance. Columellae are composed of a few, or a tight cluster of, papillary trabeculae. The undersurfaces of coralla, especially towards the perimeters, bear narrow, low, equal costae, either perfectly smooth, or with minute, blunt spines or granules.

Affinities

Coscinaraea wellsi is a discrete species which clearly includes Wells' (1954 Pl. 154) *C. ostreaeformis.* However, the latter species, as noted above (p. 94) is close to *C. columna*, of which it may be a deep water ecomorph, and hence a new name is applicable.

Wells (1954) noted that *C. donnani* Gardiner has similarities with *C. wellsi*, but the former species has a massive growth form and larger corallites with more septa. By these characters, *C. donnani* is closer to *C. monile.* All three species have weakly developed collines. *Coscinaraea wellsi* stands apart by its ill-defined corallite boundaries which are similar to those of *Psammocora*, especially *P. explanulata.* The latter very closely resembles *C. wellsi*, especially in having some circumscribed, petaloid or thamnasteroid, costae. The two species are superficially distinguished by size, *P. explanulata* having much smaller and finer skeletal structures. There may also be superficial resemblances between *C. wellsi* and *Leptoseris* species, especially *L. scabra.*

Fig. 163 *Coscinaraea wellsi* from Lord Howe Island, collecting station 143 (× 1.0).

Distribution

Known to occur in Madagascar, the Mascarene Islands, the Andaman Sea, Thailand, the Great Barrier Reef, Lord Howe Island and the Marshall Islands.

Holotype

Specimen 44818 in the United States National Museum is designated holotype of *Coscinaraea wellsi.* This specimen is figured by Wells (1954) Pl. 155, Figs. 5, 6 as *C. ostreaeformis.*

Coscinaraea crassa n. sp.

Material studied

Ashmore Reef (2 specimens from the same colony).

Previous records from Eastern Australia

Not previously recorded.

Characters

The corallum is a large, expanded irregular plate, unifacial, attached centrally to the substratum, but free on most of its undersurface, except for a small portion overgrowing a dead colony of *Lobophyllia.* It is thick and solid and very heavily calcified. The thickness gradually increases from about 5 mm at the perimeter to 40 mm in the central portion of the colony. In some places, the corallum has regrown on dead parts of the same colony. The upper surface is thamnasteroid. Colony formation is by circumoral, followed by marginal, budding. New centres are arranged in well defined rows, parallel to the corallum perimeter; older (more central) corallites are less concentric, with shorter, more irregular series. Series of corallites are 5-11 mm apart, separated by very low, irregularly developed collines, sometimes expanded into low rounded protuberances, 1-1.5 cm across, or hydnophoroid processes. Corallites are shallow. The axial fossa averages 6 mm diameter but may reach 10 mm. There are 16-22 septa in the smaller corallites, 24-32 in larger ones, of which 18-24 reach the columellae. An average of 16 (maximum 18) septo-costae per cm occur on the collines. Septo-costae mostly alternate in height and thickness. The maximum thickness is midway between corallites of adjacent series, thinning regularly towards the columellar centres. Occasionally septa of higher orders fuse with those of lower orders, giving septal groups of 2-5 (more frequently 2-3) as with other Siderastreidae. Some septo-costae are contorted (particularly those on hydnophoroid protuberances), coiled in a spiral or even completely folded, giving a petaloid shape. Septal margins are covered with single, or (more often) compound granules. An upward projecting lobe often occurs on petaloid structures just before the septa plunge towards the columella, and on septo-costae on the collines. Septal sides are heavily granulated; their upper part has few perforations. The floor of the axial fossa is a nearly solid plate, originating from a more or less complete fusion of the axial trabeculae. Columellae may be almost completely lacking to well developed and vary from one laterally compressed papillary trabecula to a linear series of 3-4 granules fused together in a lamellar process up to 4 mm in length. The corallite wall is visible below the collines. It is basically synapticulothecal and is composed of up to 4 irregular rows of synapticulae. The undersurface of the corallum is non-epithecate.

Figs. 164-167 *Coscinaraea wellsi* (× 2.5).

Figs. 164, 167 From Lord Howe Island, collecting station 143, Fig. 167 the same corallum as Fig. 163.
Figs. 165, 166 From Big Mary Reef, collecting station 131.

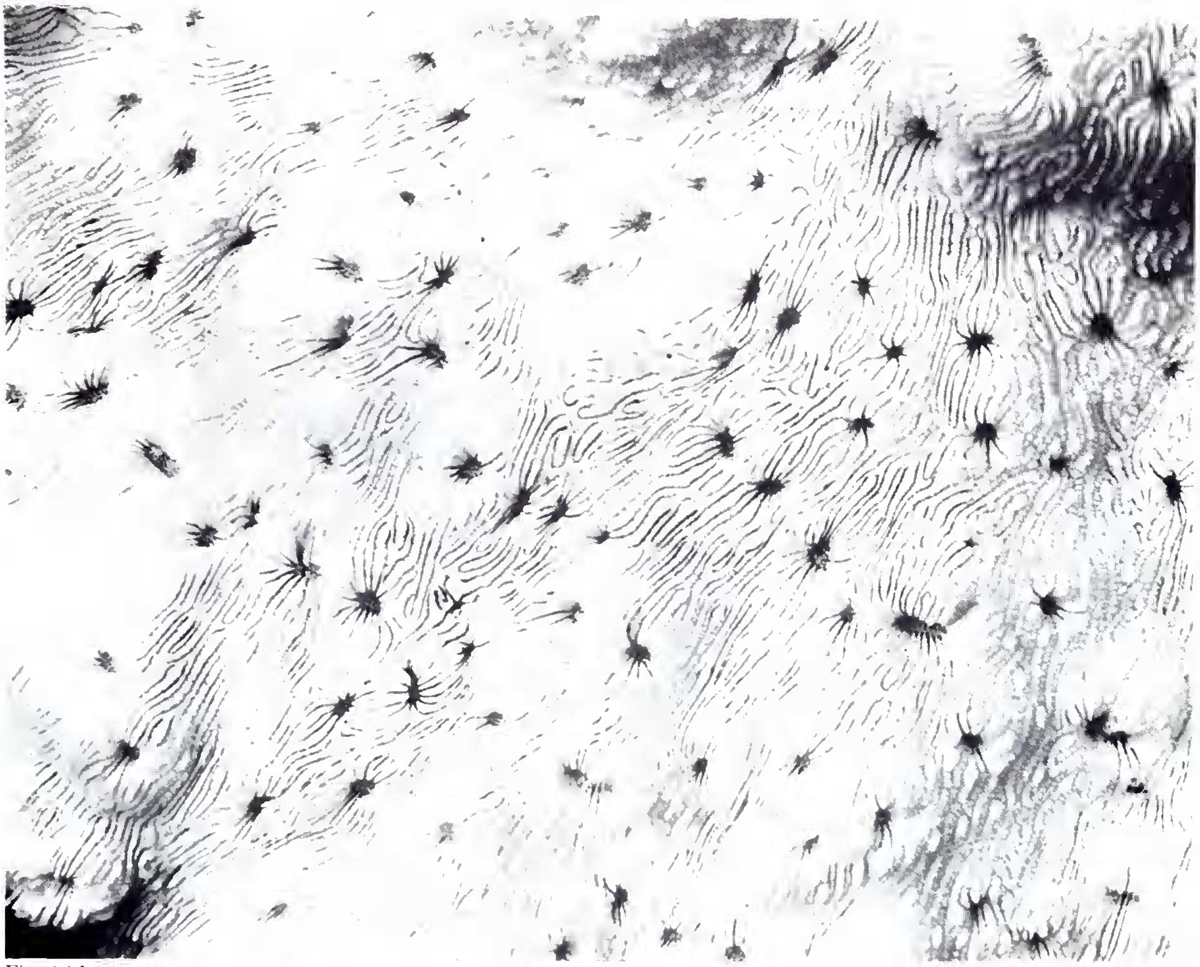


Fig. 164 ▲

Fig. 165 ▼

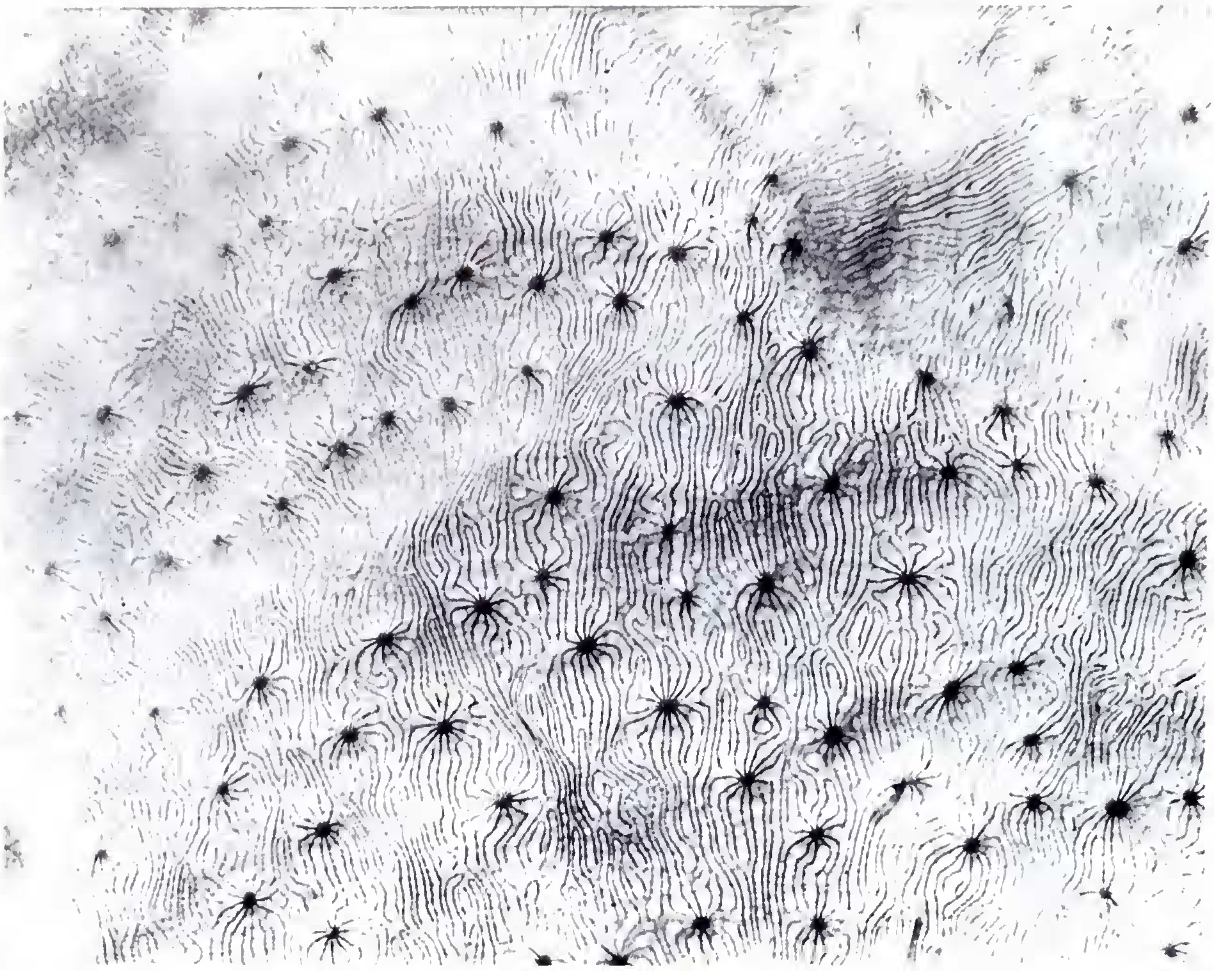
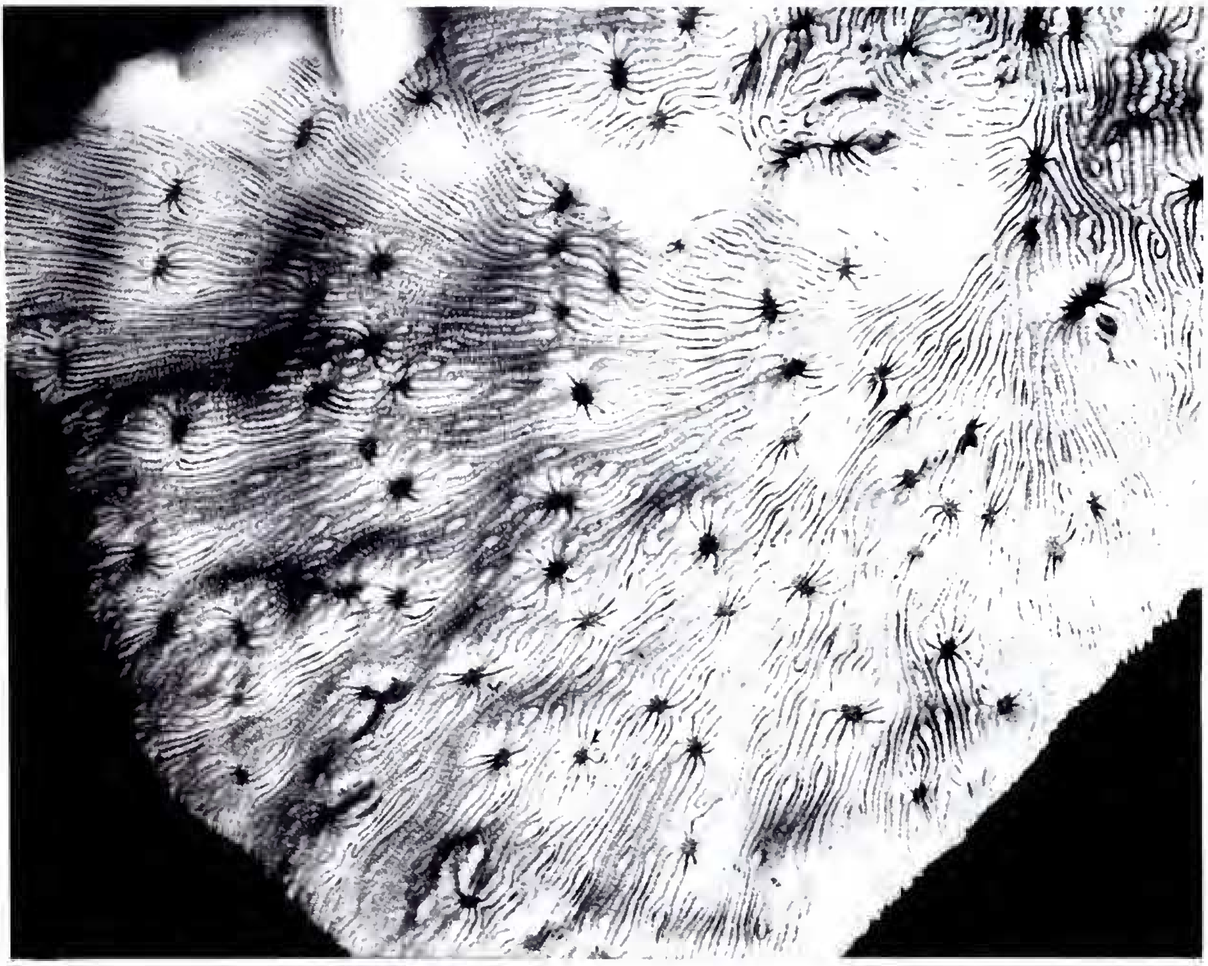


Fig. 166 ▲

Fig. 167 ▼


Costae are present in the marginal part of the colony. They are low, comparatively wide and bear scattered costal spines, with blunt, granular tops. Costae are separated by grooves with a flat floor, perforated by slit-like pores. Towards the centre of the corallum, costae become lower and disappear. Blunt costal spines and perforations are then still visible but have no definite pattern. The wall is dense and solid, with a smooth, even surface. Some parts of the undersurface are dead and encrusted.

Affinities

By the size of its skeletal structures, *C. crassa* resembles coarser specimens of *Podabacia crustacea* but septal ornamentations of the two species are clearly different. It is placed in *Coscinaraea* because of the structure and ornamentation of the septa, the structure of the columellae and the clustering of septa into groups. Its nearest ally is *C. mcneilli*, of which *C. crassa* is at least superficially a greatly enlarged, coarser and thicker version. However, *C. crassa* does not closely resemble any other species and its proper taxonomic position remains obscure.

Etymology

Named because of the thickness of the corallum and skeletal structures when compared with other species of the genus.

Holotype (Figs. 168-170)

Dimensions: 25 × 18 × 5 cm. Part of a colony approximately 1.5 m across.

Locality: Ashmore Reef, eastern Torres Strait.

Depth: 10 m.

Collector: J. E. N. Veron.

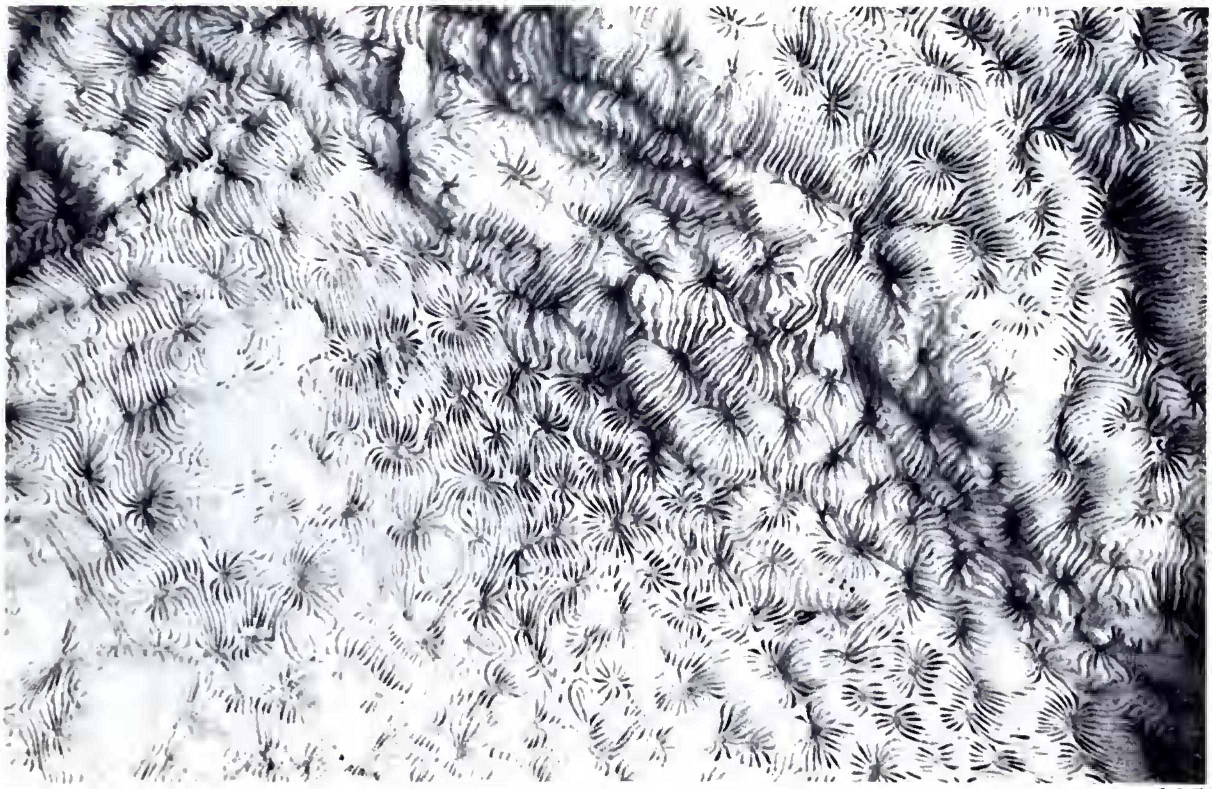
Holotype: British Museum (Natural History).

Paratype

Australian Institute of Marine Science

Figs. 168-170 Same corallum of *Coscinaraea crassa* from Ashmore Reef, collecting station 107. Fig. 168 (× 1.0), Fig. 169 (× 2.5), Fig. 170 (× 5.0).

Fig. 168 ▼



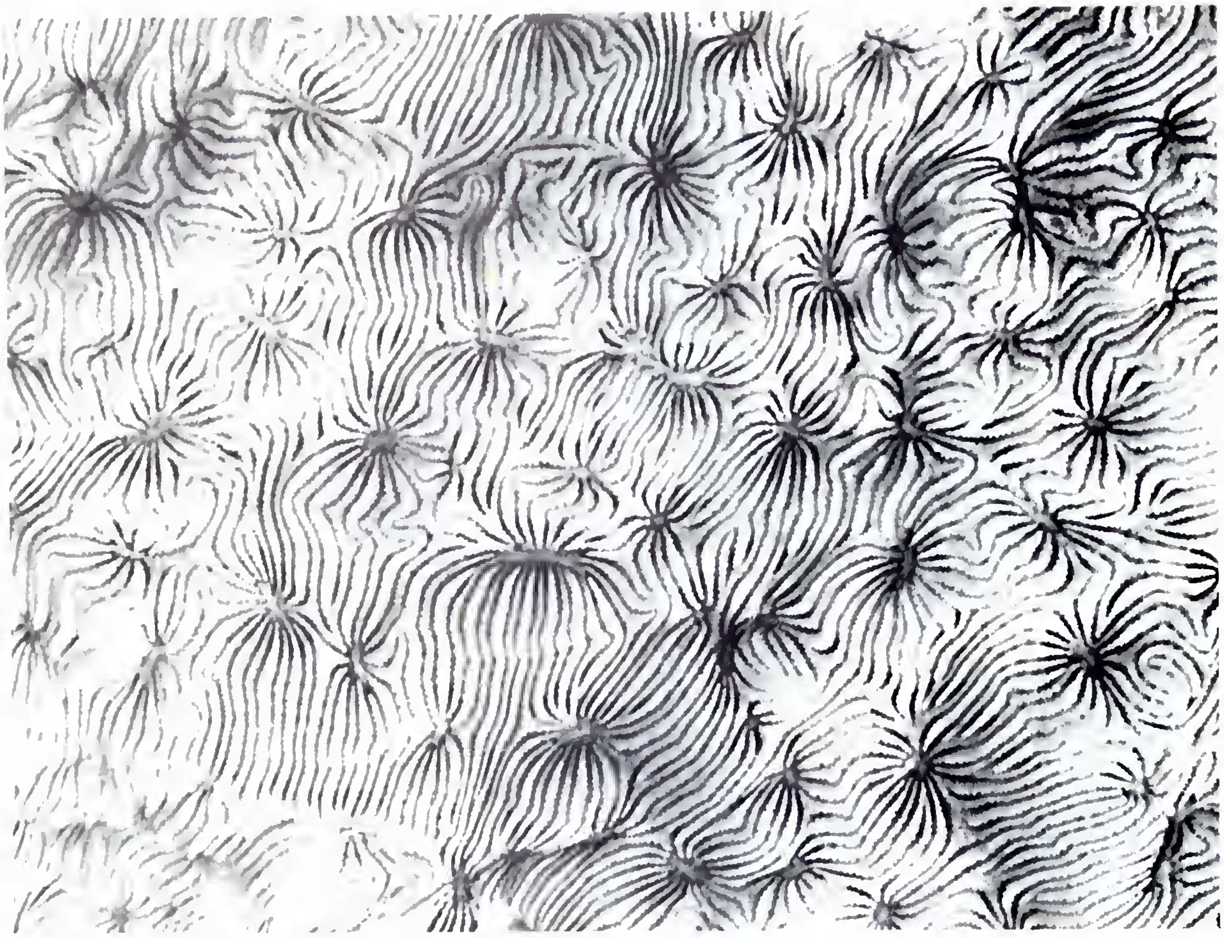
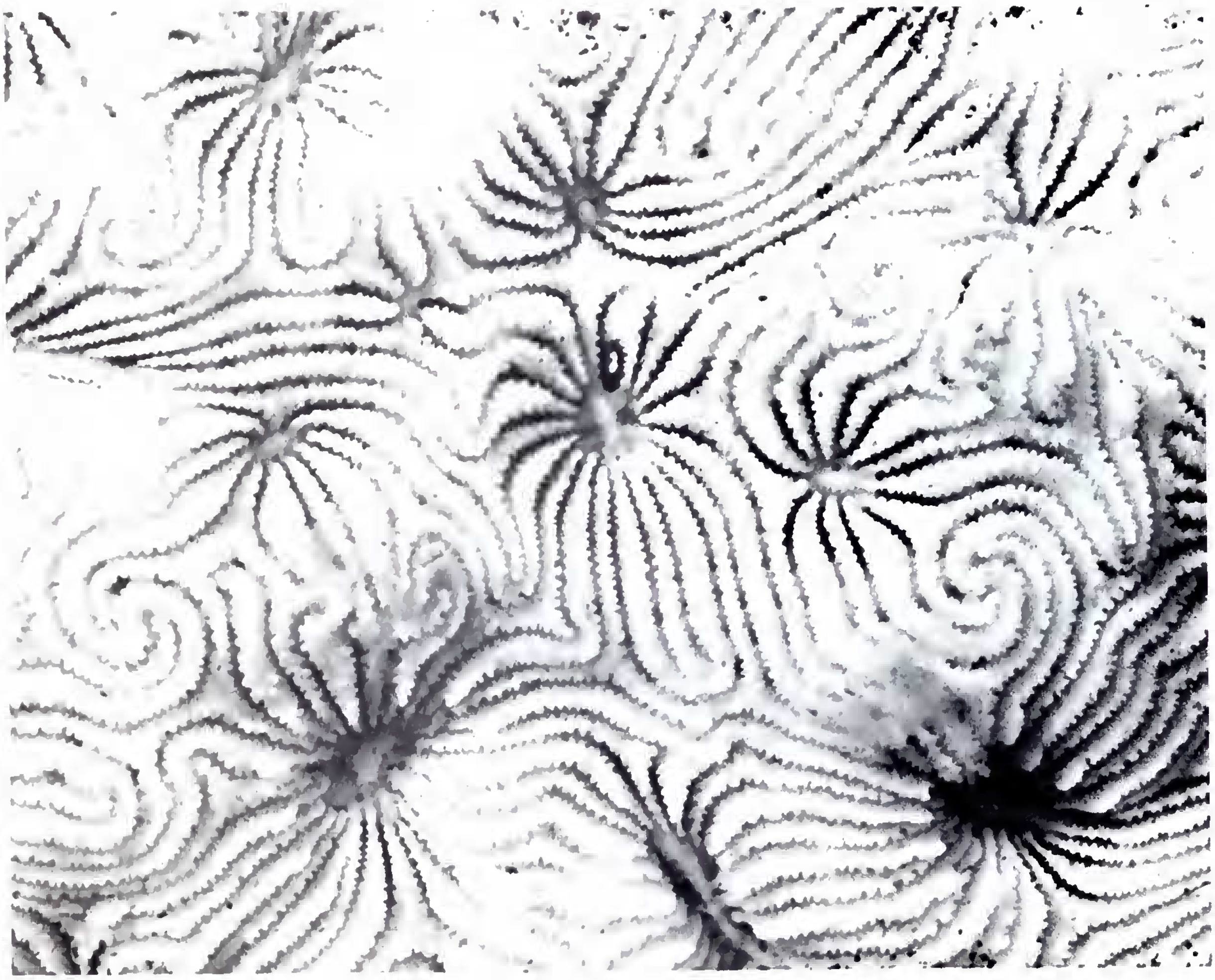


Fig. 169 ▲

Fig. 170 ▼



V
Family Fungiidae Dana, 1846

Owing to the distinctive characters of its members, the family Fungiidae is one of the very few in which species can be traced back to the pre-Linnaean literature (Tournefort, 1706; Rumphius, 1750). However, this did not help in avoiding the confusion which accompanied the first few decades of the Linnaean binomial system. Instead, and perhaps because of, the comparatively high number of early references to inadequately described or figured species, the synonymies of some species at least, remain uncertain.

The Fungiidae includes both colonial forms and the mushroom-shaped, monostomatous, free living corals of the genera *Cycloseris, Diaseris, Fungia* and *Heliofungia*. Although these genera are fundamentally monostomatous, there is an incipient tendency to develop several mouths, e.g. in *Fungia moluccensis* and related species. This evolutionary trend towards coloniality is further developed in other genera into totally polycentric conditions. Thus, Wells (1966) has shown that all colonial fungiids are derived from the solitary genus *Cycloseris* or else from four of the five subgenera of *Fungia*, and have inherited the septo-costal structures of their predecessors.

A characteristic feature of the Fungiidae is their reproductive cycle, which involves the sexual or asexual production of anthocauli from which anthocyathi detach and become free adults (except in *Lithophyllon* and *Podabacia*, which remain attached during the adult, colonial stage). The importance of this form of asexual reproduction in fungiid corals is seen when anthocauli develop in large numbers on large, often senile or partly dead specimens (Fig. 757). Similarly, the regenerative capacity of fungiid corals is considerable. All species are potentially capable of regenerating whole specimens from one fragment, either after natural radial autotomy (in *Diaseris*), or after accidental mechanical fracture. Growth forms of regenerated specimens are either similar to the usual growth form of the species (although often displaying discontinuities in the direction of the septa) or they take very irregular and complex shapes, particularly in normally elongate species. Although the skeletal structures of fungiid corals have been reasonably well studied in the past (Duncan 1884, Bourne 1887, Boschma 1934), much remains to be understood about the structure and function of the soft parts, particularly in the development of coloniality.

All genera and subgenera of the Fungiidae are present on the Great Barrier Reef with the exception of *Zoopilus*, known only from Banda, New Guinea, the Philippines, Fiji and the Marshall Islands. At present, the Great Barrier Reef Fungiidae include 33 species of 11 genera, all of which are conspicuously absent from the southern reefs of Lord Howe and the Solitary Islands.

GENUS *CYCLOSERIS* EDWARDS & HAIME, 1849

Generic synonymy

Fungia; Gardiner (1905, 1909); Döderlein (1902); Vaughan (1907); Boschma (1925).

Cycloseris Edwards & Haime, 1849c; Yabe & Sugiyama (1941); Vaughan & Wells (1943).

Type species *Fungia cyclolites* Lamarck, 1816.

Characters of the genus

Coralla are circular or slightly oval, free, mostly monastomatous, but never elongate, generally smaller than in *Fungia*, imperforate. Septal dentations are very small and numerous. Costae are distinct, finely dentate or spinose.

Introduction

Cycloseris was established by Edwards and Haime to separate a number of fossil and living species with a solid wall structure from *Fungia*. However, the consensus of opinion resulting from the detailed studies of Döderlein (1902), Gardiner (1905, 1909), Vaughan (1907) and Boschma (1925) was to unite *Cycloseris* and *Diaseris* (see p. 121) with *Fungia*. Wells (1966) separated them again on palaeontological and structural grounds. According to Wells, *Cycloseris* is the earliest member of the family Fungiidae, and the predecessor of *Fungia*. It has primitive characters, such as an imperforate wall, simple septal structures and small dentations.

Although most species of *Cycloseris* are, in adult stage, smaller than any *Fungia* species (with the possible exception of *F. cooperi*, the taxonomic status of which remains doubtful) some, e.g. *C. somervillei* and *C. patelliformis*, can be >10 cm diameter.

Some species of *Cycloseris*, notably *C. cyclolites* and *C. patelliformis*, are widespread and abundant; others are poorly known and hence have doubtful taxonomic positions. Such doubtful species include, in particular, *Fungia glans* Dana, *Cycloseris discus* Quelch and *Cycloseris mycoides* Alcock, none of which are mentioned in Döderlein's monograph. Seven species of *Cycloseris* are in the present collections. These do not include two other species of *Cycloseris* recorded by Tenison-Woods (1879a) from northeast Australia: *C. hexagonalis* Edwards & Haime and *C. sinensis* Edwards & Haime, the latter from Princess Charlotte Bay.

Cycloseris cyclolites (Lamarck, 1801)

Synonymy

Fungia cyclolites Lamarck, 1801; Lamarck (1816); Döderlein (1902); Gravier (1907, 1911); Gardiner (1909); Harrison & Poole (1909b); Folkeson (1919); (*pars*) van der Horst (1921); Matthai (1924); Boschma (1925); Faustino (1927); Yabe & Sugiyama (1932, 1935, 1941); Rossi (1954).

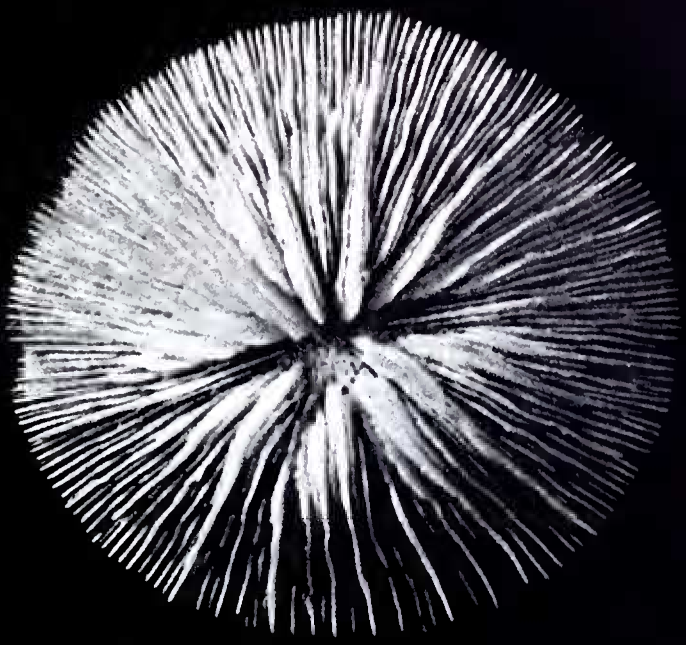
Cycloseris cyclolites (Lamarck); Edwards & Haime (1851a, 1851c, 1860); Studer (1877); Tenison-Woods (1878); Quelch (1886); Saville-Kent (1893); Gardiner (1905); Crossland (1952); Nemenzo (1955a); Wells (1955b, 1964b); Boschma (1959); Eguchi (1968); Scheer & Pillai (1974).

Diaseris mortoni Tenison-Woods, 1880b.

Material studied

Localities between **Lizard Island** and **Bramble Cay** (41 specimens), **Lizard Island** (31 specimens), **Palm Islands** (24 specimens), **Bowling Green Bay, Heron Island** (16 specimens).

Figs. 171-174 *Cycloseris cyclolites* from the Palm Islands (× 2.5). Figs. 171, 173, same corallum; Figs. 172, 174, same corallum.



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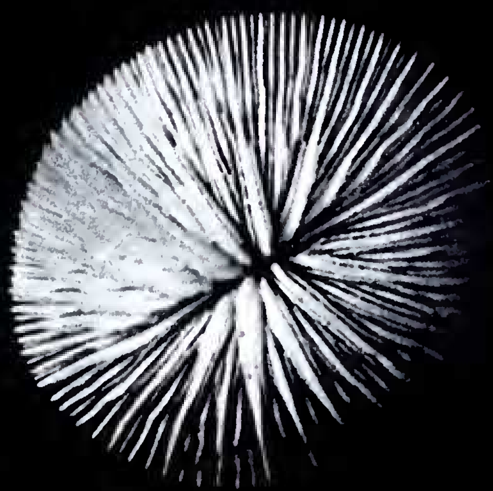


172

174

Previous records from Eastern Australia

Moreton Bay, Wells (1955b); **Moreton Bay** to **Michelmas Cay**, Wells (1964b); **Harvey Bay,** Tenison-Woods (1878); **Lady Elliott Island,** Tenison-Woods (1878); **Holbourne Island** (as *Diaseris mortoni*), Tenison-Woods (1880b); **Magnetic Island,** Wells (1955b); **Palm Islands,** Wells (1955b); **Low Isles,** Crossland (1952); **Lizard Island,** Yonge (1930), Goreau & Yonge (1968).

Characters

Coralla are circular or slightly oval, up to 41 mm maximum diameter and 18 mm in height. The undersurface is strongly concave to almost flat, the oral surface is strongly convex with the septal margins of some coralla becoming almost vertical at the periphery. Septa are equal towards the periphery but those of the first two orders become conspicuously higher towards the central part of the corallum. The inner margins of the first and second septal orders are vertical. They bear minute triangular dentations, averaging 0.4 mm. Septa of higher orders have irregular ornamentations. The sides of septa have small, pointed granules arranged in trabecular rows, each row corresponding to a dentation. The mouth fossa is usually elongate, the columellae are weakly developed. The undersurface is covered with thin, equal, or regularly alternating, costae. These bear numerous, regular, small blunt spines, or rounded granules. They become slightly wavy and ill defined towards the centre but retain their spines or granules. The centre of the undersurface has a low boss in the position of the scar of attachment (which is not visible).

When extended, tentacles resemble those of *Fungia* spp. (Fig. 753).

Skeletal variation

The present series, of approximately 110 specimens, displays almost no variation except in corallum size. Collections from several other Indo-Pacific localities similarly display very stable skeletal characteristics. However, Boschma's (1925) series from Ambon shows a high variability, perhaps as a result of the proximity of the Galala River mouth creating an unstable environment.

Affinities

Cycloseris cyclolites is a clearly defined species although it has been confused with other *Cycloseris* notably *C. somervillei* and *C. costulata* (e.g. van der Horst, 1921; Pl. 2, Fig. 5).

Affinities with *C. somervillei* are discussed with the latter species. *Cycloseris elegans*, which seems to belong to the same group of species, is apparently restricted to the eastern Pacific.

Distribution

Recorded from the Red Sea, Ceylon, south India, the Andaman and Nicobar Islands, the Mergui Archipelago, Indonesia, the Philippines, the Great Barrier Reef, New Britain, Japan and Palau.

Cycloseris costulata (Ortmann, 1889)

Synonymy

Fungia costulata Ortmann, 1889; Döderlein (1902); Gardiner (1909).

Cycloseris cyclolites (Lamarck); *sensu* Gardiner 1905 (*pars*).

Fungia cyclolites (Lamarck); *sensu* van der Horst (1921) (*pars*).

Fungia doderleini Yabe & Sugiyama, 1941; *non* von Marenzeller (1907).

Cycloseris costulata (Ortmann); Pillai & Scheer (1976).

Material studied

Murray Islands, MacGillivray Reef.

These localities include collecting stations 29, 74.

Previous records from Eastern Australia

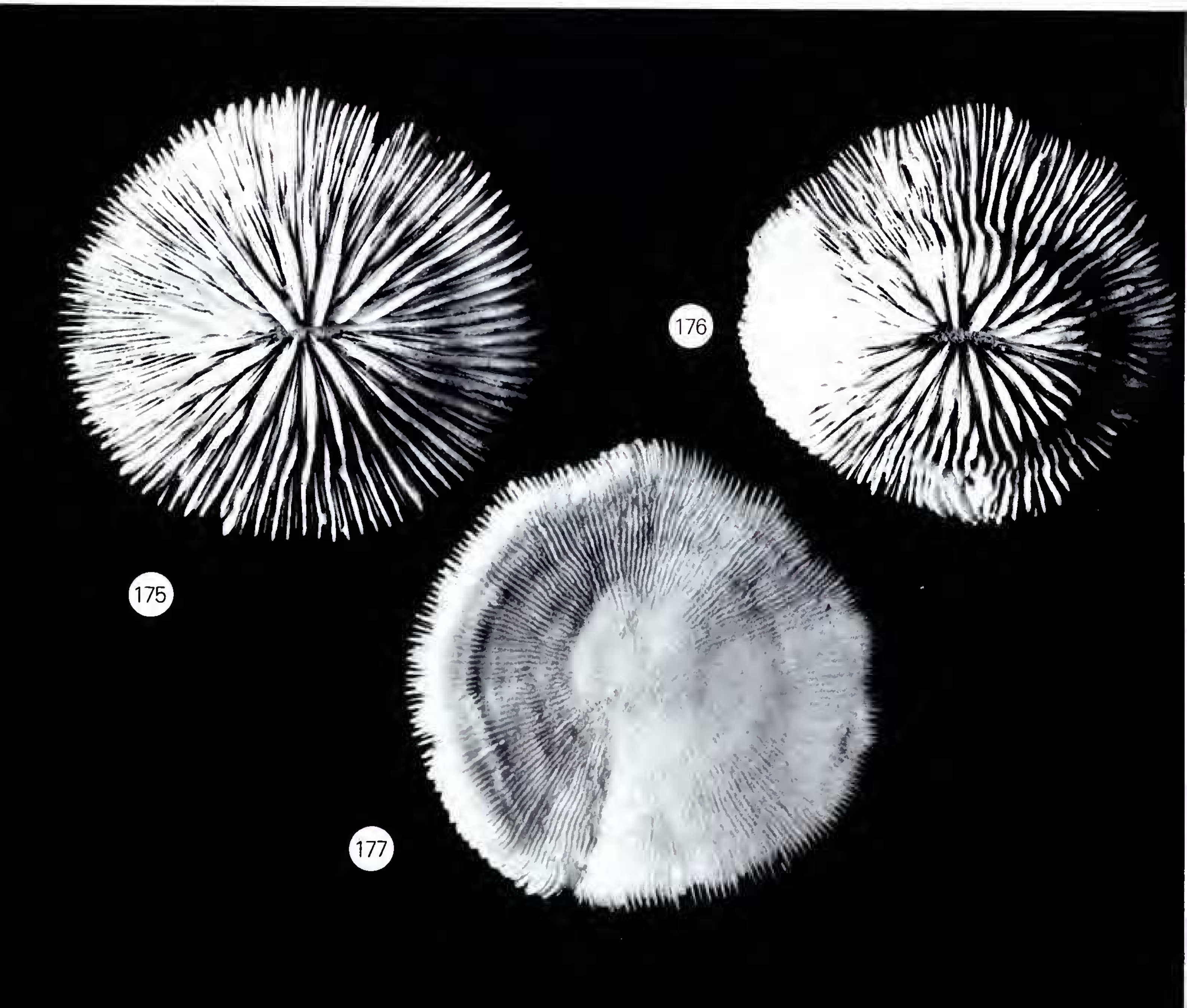
Not previously recorded.

Characters

Coralla are circular, up to 7.6 cm diameter. The undersurface is slightly concave; the upper surface is convex, with the central part arched around the central fossa. Septa are unequal; those of the first two or three orders are relatively exsert, markedly so in the arched inner half of the upper surface, only slightly so at the corallum periphery. Low order septa increase in thickness towards the mouth. Septal margins have very small, subtriangular, irregular dentations. The upper part of septa are porous to varying degrees and granular. The undersurface is covered with well defined, laminar costae which radiate almost from the corallum centre. Their upper margin is covered with a dense series of short, irregular spines or granules which can be followed to the centre of the undersurface. The wall is imperforate.

Figs. 175-177 *Cycloseris costulata* (× 1.0).

Fig. 175 From Dewar Island, collecting station 29.
Figs. 176, 177 Same corallum from MacGillivray Reef, collecting station 74.



Affinities

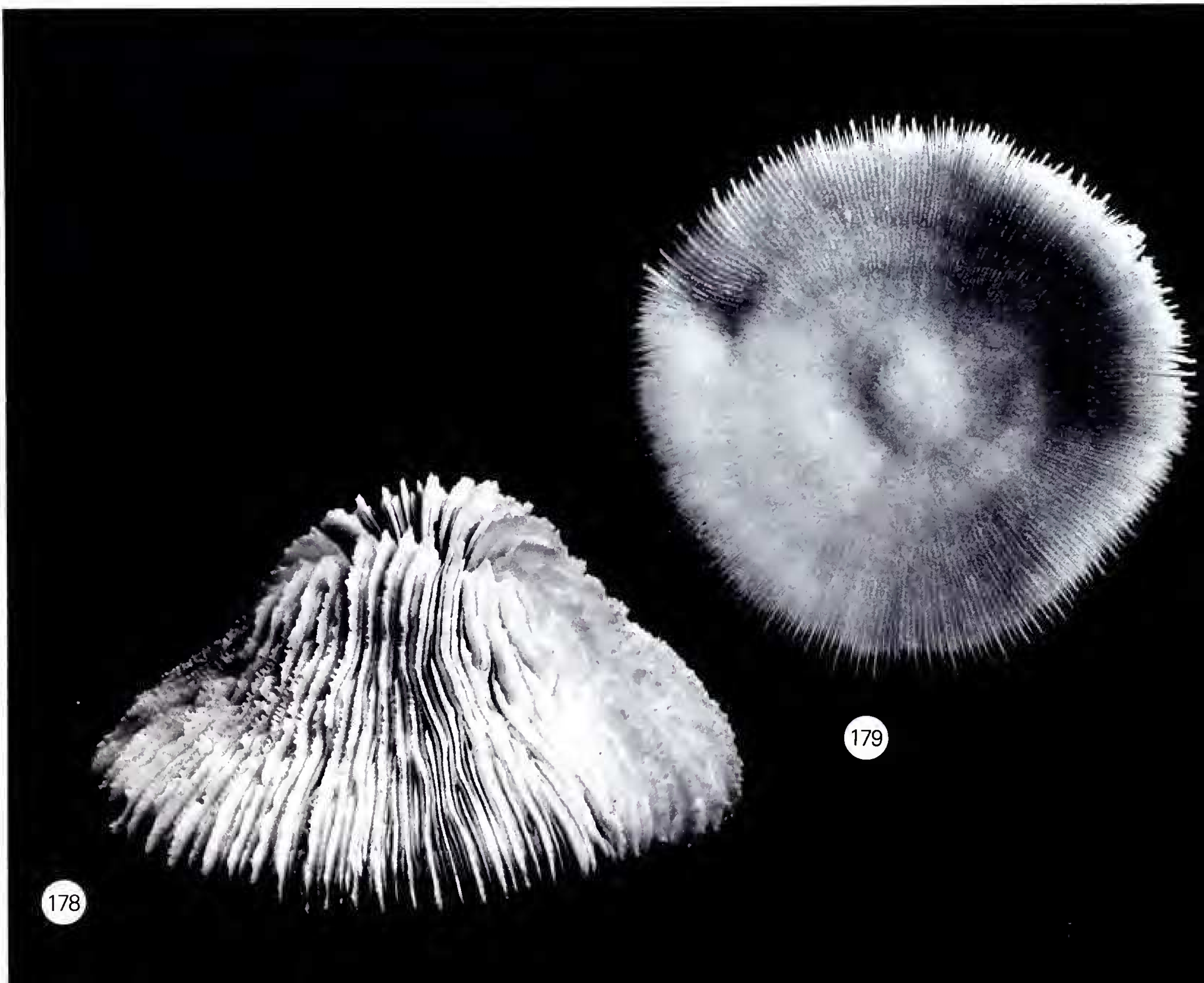
Cycloseris costulata is closest to *C. cyclolites*, both having small, numerous, very distinct, parallel-edged costae. Their differences are appropriately summarised by Pillai & Scheer (1976). In *C. costulata*, costae are straight with prominent but small spines or frosted granules and extend to the centre of the corallum. In *C. cyclolites* costae are wavy towards the centre and generally bear rounded granules. They are further distinguished by differences in the size and symmetry of the skeleton, which is more variable in *C. costulata* and smaller, more regular and highly convex in *C. cyclolites*.

Gardiner (1909) doubted the specific identity of *Fungia costulata* Ortmann and *Fungia costulata* Döderlein and Yabe & Sugiyama (1941) gave the name *doderleini* to the latter. Neither Gardiner nor Yabe & Sugiyama, however, gave any basis for their distinctions, and their descriptions and figures of both supposed species are not substantially different.

Distribution

Recorded from the Maldive Islands, Ceylon, the Great Barrier Reef, the Bismarck Archipelago and Palau.

Figs. 178, 179 *Cycloseris erosa* (× 1.0), same corallum from Lizard Island Lagoon, collecting station 99.



Cycloseris erosa (Döderlein, 1901)

Synonymy

Fungia erosa Döderlein, 1901; Döderlein (1902); van der Horst (1921); Yabe & Sugiyama (1941).

Material studied

Lizard Island, Plug Reef, Frigate Cay.

These localities include collecting stations 32, 64, 81, 99.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are circular or subcircular, up to 8.5 cm diameter. The undersurface is flat or slightly concave, the upper surface is flat, with the central part slightly arched around the central fossa or strongly convex (Fig. 178). Septa are unequal; those of lower orders slightly increase in thickness towards the centre, those of higher orders decrease in height at the point of fusion with septa of the next highest order. A weak tentacular lobe may be present just before the point of decrease in height. Septal margins are laciniate and ragged, composed of irregularly contorted spiny processes. In rare instances where septal margins are entire, they bear small, regularly triangular dentations. The upper septal sides are perforated, the lower parts are covered with granules or spines. The margins and sides of higher orders are granular. Costae are only well developed towards the periphery where they are cyclically unequal and laminar. They become slightly wavy towards the centre, then disappear completely. All costae are ornamented with small granules or spines which decrease in size from the periphery towards the centre. Walls are not perforate.

Skeletal variation

Apart from the shape of the corallum, the only variations observed in *C. erosa* are in the degree of perforation and laciniate character of the septa, and in the degree of development of the costae.

Affinities

Superficially, the characters of the upper surface of *C. erosa* come close to those of *C. patelliformis*, but they differ markedly in the characters of the septal margins and of the costae. *Cycloseris laciniosa* Boschma, 1925, has similar septal structures. According to Boschma, it differs from *C. erosa* in having less prominent costae and very thick, spongy septa. The validity of *C. laciniosa* as a separate species, however, remains doubtful.

Döderlein considered *C. erosa* to be a direct but remote derivative from his '*patella*' group of species including *C. patelliformis, C. fragilis, C. tenuis,* and *C. hexagonalis.*

Distribution

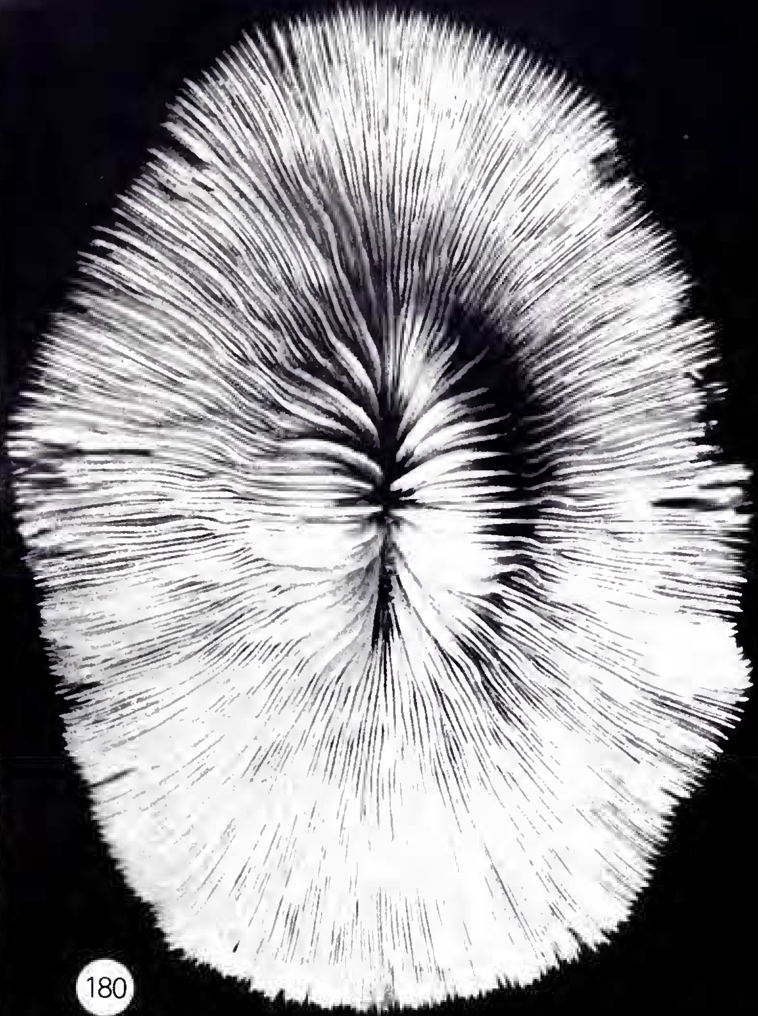
This apparently rare species is known only from Japan, Indonesia and the Great Barrier Reef.

Cycloseris somervillei (Gardiner, 1909)

Synonymy

Fungia somervillei Gardiner, 1909; van der Horst (1921); (*pars*) Matthai (1924); Boschma (1925).

Cycloseris somervillei (Gardiner); (*pars*) Pillai (1972).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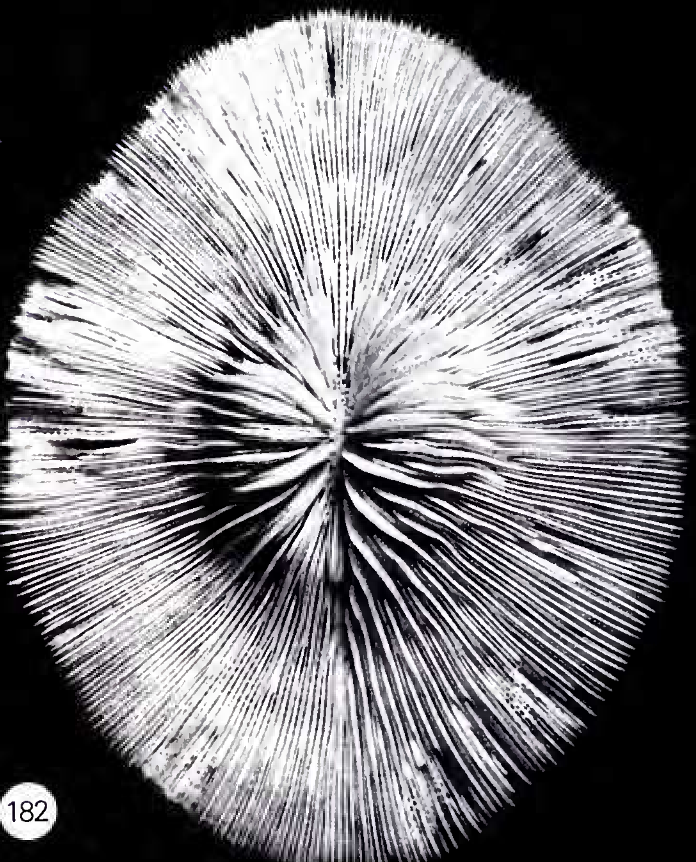

182


183

Material studied

Murray Islands.

Previous records from Eastern Australia

Not previously recorded.

Characters

The single specimen of this species in the present collection (Figs. 180, 181) is oval, 130 × 96 mm and flat, except around the central fossa which is distinctly arched. Septa are numerous and thin, except toward the centre, where those of the lower orders increase in thickness. Septal margins bear small, regular, triangular dentations, which correspond to vertical rows of small granules on the septal sides. The axial fossa is narrow and elongate. The columella is well developed and delicately spongiose. Costae are thin, slightly wavy towards the centre of the corallum and slightly alternate towards the perimeter where three orders can be recognised. On the rest of the undersurface, they are equal or sub-equal. All costae are covered with numerous, small, blunt spines.

All verified specimens of *C. somervillei* have been collected at >35 m depth.

Affinities

This specimen is similar to Gardiner's holotype (Fig. 182) and also similar to Boschma's (1925) specimen from the Sulu Islands. The affinities of *C. somervillei* were originally indicated by Gardiner (1909) who ascribes it to his '*Cycloseris*' group of species. Subsequently, Matthai (1924, in part) and Scheer & Pillai (1974) confused it with *Fungia moluccensis*, a species which stands well apart from *Cycloseris* proper.

Gardiner (1909) noted that *Fungia* (= *Cycloseris*) *sinensis* Edwards & Haime was a near ally of *F. somervillei*, the major differences being the equal to subequal size of the costae and the rounded corallum shape. *Cycloseris sinensis*, however, is a doubtful species with uncertain affinities.

Distribution

Recorded from the Seychelles, Amirante and Sulu Islands, the Great Barrier Reef and Fiji.

Cycloseris patelliformis (Boschma, 1923)

Synonymy

Fungia patella (Ellis & Solander); (*pars*) Döderlein (1902); (*pars*) van der Horst (1921); Faustino (1927).

Fungia patelliformis Boschma, 1923b; Boschma (1925); Hoffmeister (1925); Crossland (1952).

Cycloseris patelliformis (Boschma); Wells (1954); Pillai, Vine & Scheer (1973); Scheer & Pillai (1974).

Material studied

Lizard Island (35 specimens).

Previous records from Eastern Australia

Low Isles, Crossland (1952).

Figs. 180-183 *Cycloseris somervillei* (× 1.0).

Figs. 180, 181 Same corallum from Murray Island.

Figs. 182, 183 Same corallum, holotype.

Characters

Coralla are circular, or very slightly elongate, up to 7 cm maximum diameter. Broken specimens, which are common, regenerate into an almost circular corallum. The undersurface is flat or slightly concave. The upper surface is flat, except around the axial fossa, where septa of the lower orders are strongly arched (Fig. 184). Coralla usually have very thin perimeters.

Septa are numerous and thin, except for the central part of first order and some second order septa. Those of higher orders abruptly decrease in height towards the centre, to the point where they fuse with two septa of the next higher order. Septal margins are sharp and bear numerous minute dentations, inconspicuous to the naked eye. Their sides are ornamented with very small granules. Synapticulae are visible between septa in some specimens. The columella is an elongate mass of papillae. Costae are numerous, thin, clearly visible from the margins to the centre of the corallum where a scar of attachment is usually visible. In large specimens, the costae of the first two orders are slightly more elevated than the others and all bear minute, conical spines.

Cycloseris patelliformis has been found only on soft, sandy to muddy substrates.

Affinities

Boschma (1923b) showed that the synonymy of this species cannot be established prior to Döderlein (1902), owing to lack of sufficient descriptions and figures or loss of specimens. *Cycloseris patelliformis* is, however, a well defined species, characterised chiefly by the central part of lower order septa being much higher than the outer part and by the thin, sharp margins of septa. Some specimens from Samoa referred to this species by Hoffmeister (1925) have an unusually large size and elongate shape (up to 13 × 9 cm).

Distribution

Recorded from the Seychelles and Nicobar Islands, Indonesia, the Philippines, the Great Barrier Reef and Samoa. The species is reported from Hawaii by Boschma (1925), but this has not been confirmed (Maragos, 1977).

Cycloseris vaughani (Boschma, 1923)

Synonymy

Fungia patella (Ellis & Solander); *sensu* Vaughan (1907a, 1907b); Gravier (1911).

Fungia vaughani Boschma, 1923b; Boschma (1925).

Cyloseris vaughani (Boschma); Wells (1954, 1972); Maragos (1977).

Material studied

Lizard Island (4 specimens).

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are circular, the undersurface is flat, the upper surface regularly increases in height towards the central fossa. Septa are numerous. The central part of first and second order septa are markedly thickened and arched above the central fossa. Those of higher orders decrease regularly in height and length and remain unequal at the periphery. Septal margins bear very small triangular to lacerate dentations. Their sides are covered with small granules. Synapticulae are visible from above, between the septa. The undersurface is solid, imperforate, with numerous costae. These are low, very thin, and inconspicuous in the central half of the corallum. They become

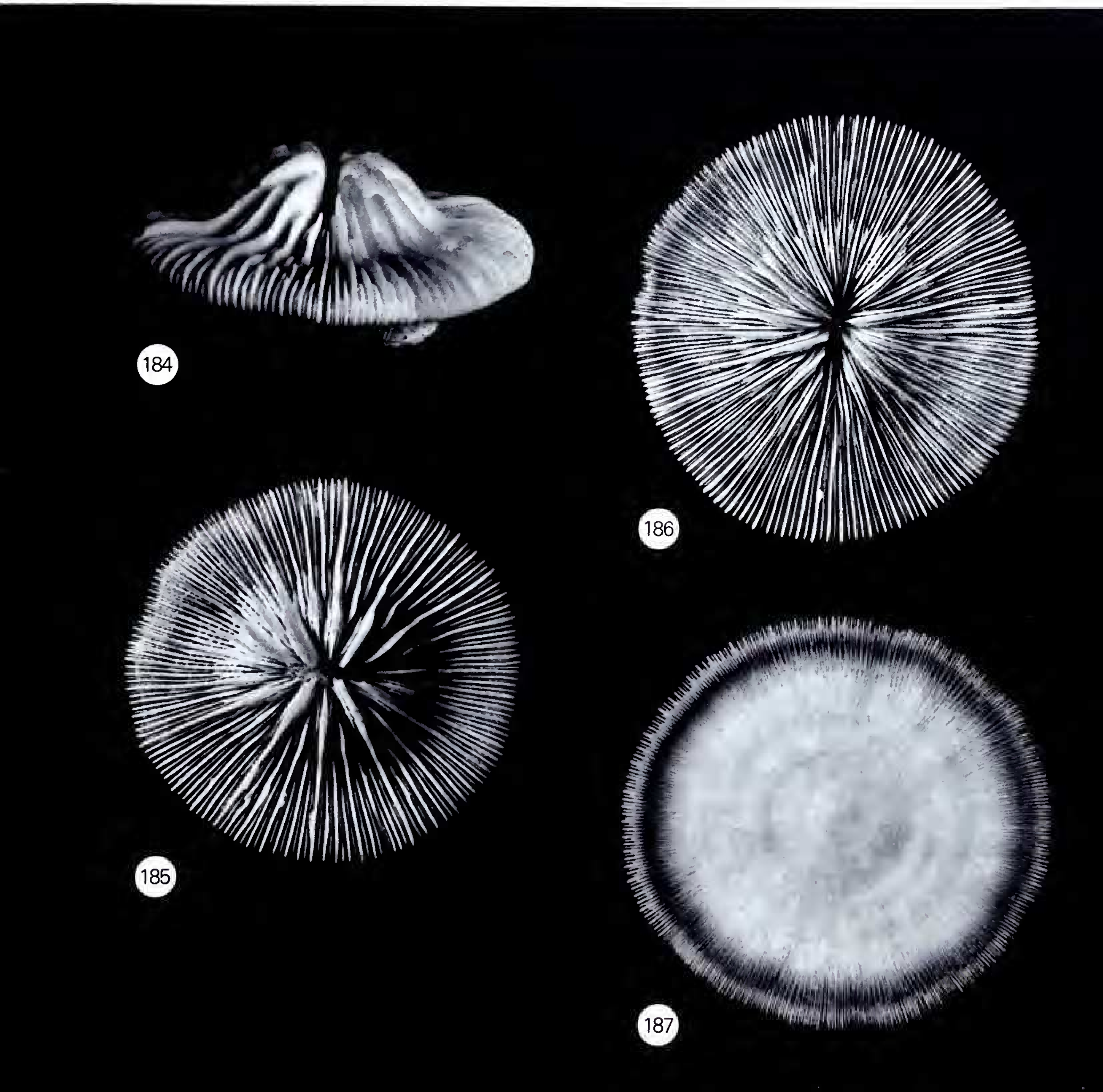
cyclically unequal towards the outer half, the principal ones being relatively thicker, higher and longer. All costae bear minute conical spines or frosted granules. A scar of attachment is not visible.

In Hawaii *C. vaughani* is found on pebble flats and hard surfaces, at depths usually greater than 15 m. The specimens of the present collection were from a flat sandy substrate.

Affinities

Although *C. vaughani* was confused with *C. patelliformis* (i.e. with *Fungia patella*) by Vaughan (1907), the former species has unequal (alternating) costae towards corallum periphery whereas the latter has equal costae. *Cycloseris patelliformis* also has a flat upper surface, with principal septa very arched above the central fossa.

Figs. 184-187 *Cycloseris patelliformis* from Lizard Island (× 1.5). Figs. 184, 185, same corallum; Figs. 186, 187, same corallum.



By the cyclical arrangement of its costae, *C. vaughani* stands apart from the *C. cyclolites* group of species (which includes *C. somervillei, C. costulata* and *C. patelliformis*) and comes close to *C. erosa* and *C. laciniata.* Their septal ornamentation, however, remains quite different.

Distribution

Known from the Nicobar Islands, Banda Sea, Paternoster Islands, the Great Barrier Reef, Bikini Atoll, Hawaii and Easter Island.

Cycloseris marginata (Boschma, 1923)

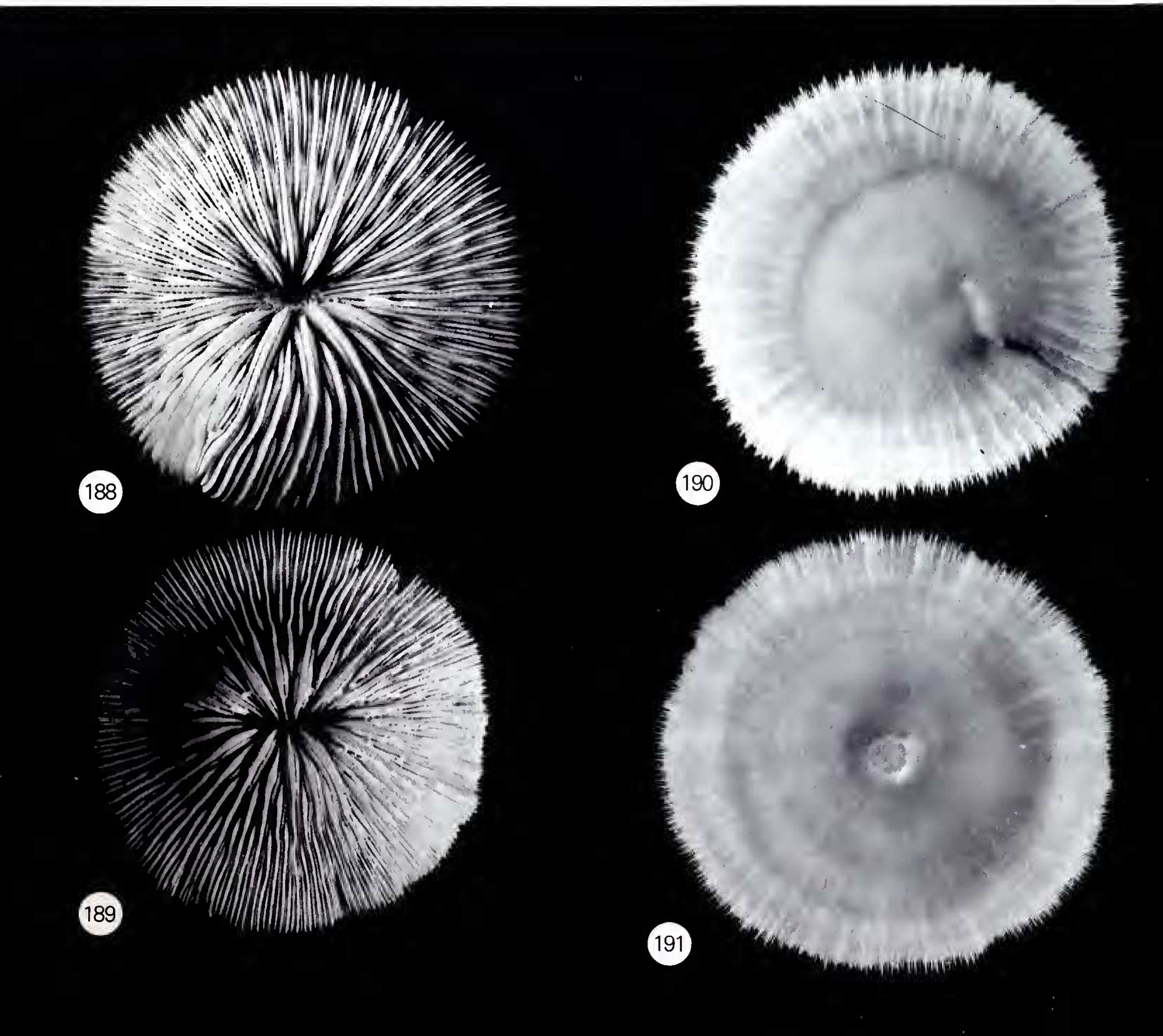
Synonymy

Fungia patella van der Horst, 1921 (*pars*).

Fungia marginata Boschma, 1923b; Boschma (1925).

Cycloseris marginata (Boschma); Scheer & Pillai (1974).

Figs. 188-191 *Cycloseris vaughani* from Lizard Island (× 1.3). Figs. 188, 190, same corallum; Figs. 189, 191, same corallum.



Material studied

Lizard Island.

Previous records from Eastern Australia

Not previously recorded.

Characters

The single specimen in the present collections is discoidal, irregularly circular in outline. The upper surface is slightly hollow, septal margins being concave in the region between the centre and the margin. The undersurface is convex except at the periphery where it is slightly curved downwards. The corallum margins are thick and rounded. Septa are regularly and clearly arranged in markedly different orders. Those of higher orders abruptly decrease in height when fusing with septa of next highest order. The outer part of the septa of all orders (before fusion) are equal in height and thickness, except for those of the highest order, which are relatively thin. Septal margins are comparatively thick, with blunt margins covered with numerous minute dentations or granules. The sides of septa are strongly granulated. The central fossa is deep; its length is 3 times the width. The columella is completely lacking. The undersurface bears well developed, lamellar costae in the outer part which become lower and disappear towards the corallum centre. A scar of attachment is visible. Costae are cyclically unequal towards the margin of the corallum, every fourth costa being higher than the others. They are all covered with numerous minute spines with pointed tips. Costal spines are smaller and without defined arrangement towards the corallum centre.

Affinities

The present specimen differs from Boschma's description only in two characters: the lower margin is curved downwards, and the scar of attachment is clearly visible. Otherwise, the characters are in every respect similar.

Boschma discussed the affinities of *C. marginata* with *Fungia costulata* Ortmann and *Fungia costulata* Döderlein. Although there is a superficial resemblance between these, both Ortmann's and Döderlein's specimen, have better developed, equal costae, which almost reach the corallum centre.

Distribution

Recorded from the Red Sea, the Gulf of Aden, the Mascarene Archipelago, the Great Barrier Reef and Hawaii.

GENUS *DIASERIS* EDWARDS & HAIME, 1849

Generic synonymy

Fungia; (pars) Michelin (1843); Döderlein (1902); Gardiner (1909); van der Horst (1921); Boschma (1923b, 1925, 1929); Matthai (1924).

Diaseris Edwards & Haime, 1849c; Gardiner (1905).

Cycloseris; (pars) Quelch (1886).

Type species *Fungia distorta* Michelin, 1843.

Characters of the genus

Coralla are free, discoidal, flat, composed of several wedge-shaped segments, which are more or less completely separate from each other. The wall is imperforate. Septa are thick, with blunt margins, ornamented with small, irregularly triangular dentations or granules. Costae are thin, lightly and delicately spinulose.

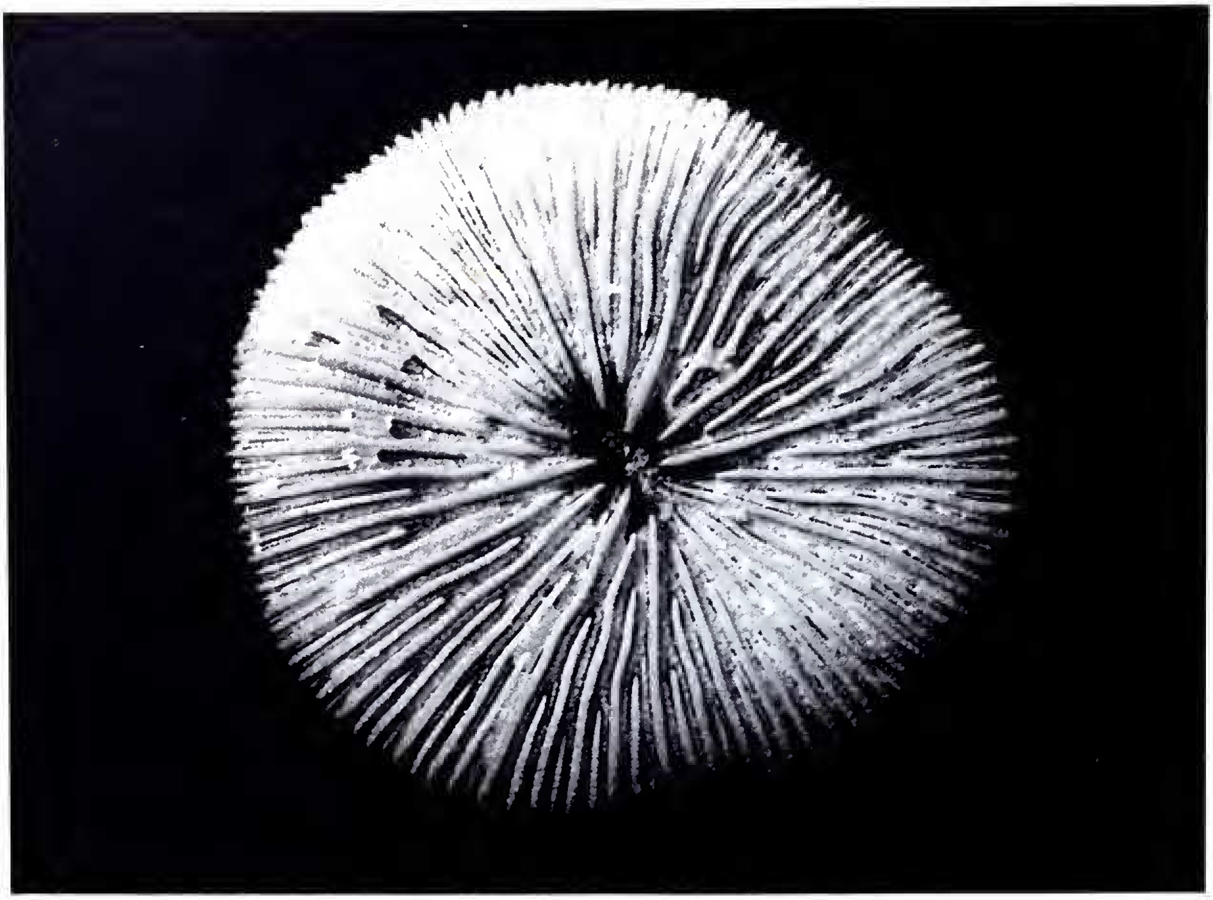


Fig. 192 ▲

Figs. 192, 193 *Cycloseris marginata*, same corallum from Lizard Island (× 2.0).

Fig. 193 ▼

Introduction

There has been much confusion in the literature between *Diaseris* and *Cycloseris*. In particular, a number of nominal species of the *patella* group have been reported as both *Cycloseris* and *Diaseris* forms or species. These were defined by Döderlein as follows: 'Disc single, entire, round, oval or conspicuously arched (*Cycloseris* form) or showing spontaneous division, or in process of regeneration (*Diaseris* form)'. Thus, specimens had to have an entire corallum to be classified as *Cycloseris*. However, regeneration after being damaged is not uncommon in *Cycloseris*, particularly in the lightly calcified species such as *C. patelliformis*. This is quite a different process from the tendency of *Diaseris* to keep splitting into equal or subequal segments as a means of asexual reproduction.

The following five species have been ascribed to *Diaseris* by Döderlein (1902) and Vaughan (1907): *distorta* Michelin, *freycineti* Edwards & Haime, *pulchella* Verrill, *mortoni* Tenison-Woods and *fragilis* Alcock. Of these, *D. freycineti* is synonymous with *D. distorta*, and *D. mortoni* is synonymous with *C. cyclolites*. *Diaseris pulchella*, described from Japan by Verrill, is cited but not discussed by Döderlein and it is not recorded by Yabe & Sugiyama (1941). The remaining two species, *D. distorta* and *D. fragilis*, are in the present collections.

Diaseris distorta (Michelin, 1843)

Synonymy

Fungia distorta Michelin, 1843; Döderlein (1902); von Marenzeller (1907); Gardiner (1909); Boschma (1923b, 1925, 1929); Matthai (1924); Faustino (1927).

Cycloseris distorta (Michelin); Quelch (1886); Bassett-Smith (1890); Ortmann (1892); Wells (1954).

Diaseris distorta (Michelin); Edwards & Haime (1851a, 1860); Semper (1872); Alcock (1893); Gardiner (1905); Harrison & Poole (1909a); Goreau & Yonge (1968).

Diaseris freycineti Edwards & Haime, 1851a; Edwards & Haime (1860); Semper (1872); Alcock (1893).

Cycloseris freycineti (Edwards & Haime); Bassett-Smith (1890).

Fungia patella (Ellis & Solander); (*pars*) Döderlein (1902); (*pars*) van der Horst (1921).

Fungia freycineti (Edwards & Haime); Faustino (1927).

Cycloseris fragilis (Alcock); *sensu* Maragos (1977).

Material Studied

Murray Islands (26 specimens), **Lizard Island** (2 specimens), **Palm Island, Bushy Island-Redbill Reef** (6 specimens).

These localities include collecting stations 56, 128, 130, 131.

Previous records from Eastern Australia

Lizard Island, Goreau & Yonge (1968), Goreau & Goreau (1969); **Heron Island,** Eguchi & Woodhead (1969).

Characters

Coralla are discoidal, up to 4 cm across, and are composed of several (usually 3 to 6) wedge-shaped sectors which regularly break apart as a means of reproduction. The margins of these sectors may be in several straight-edged segments or are regularly rounded. Various stages of splitting are observed between the sectors, from a narrow groove starting from marginal incisions which limit the sectors, to sectors

which are only connected to the remainder of the corallum by their inner end. The undersurface is either flat or slightly concave. The upper surface is either slightly convex, or slightly depressed towards the mid-radius area. Coralla peripheries are relatively thick (up to 4 mm in the larger specimens).

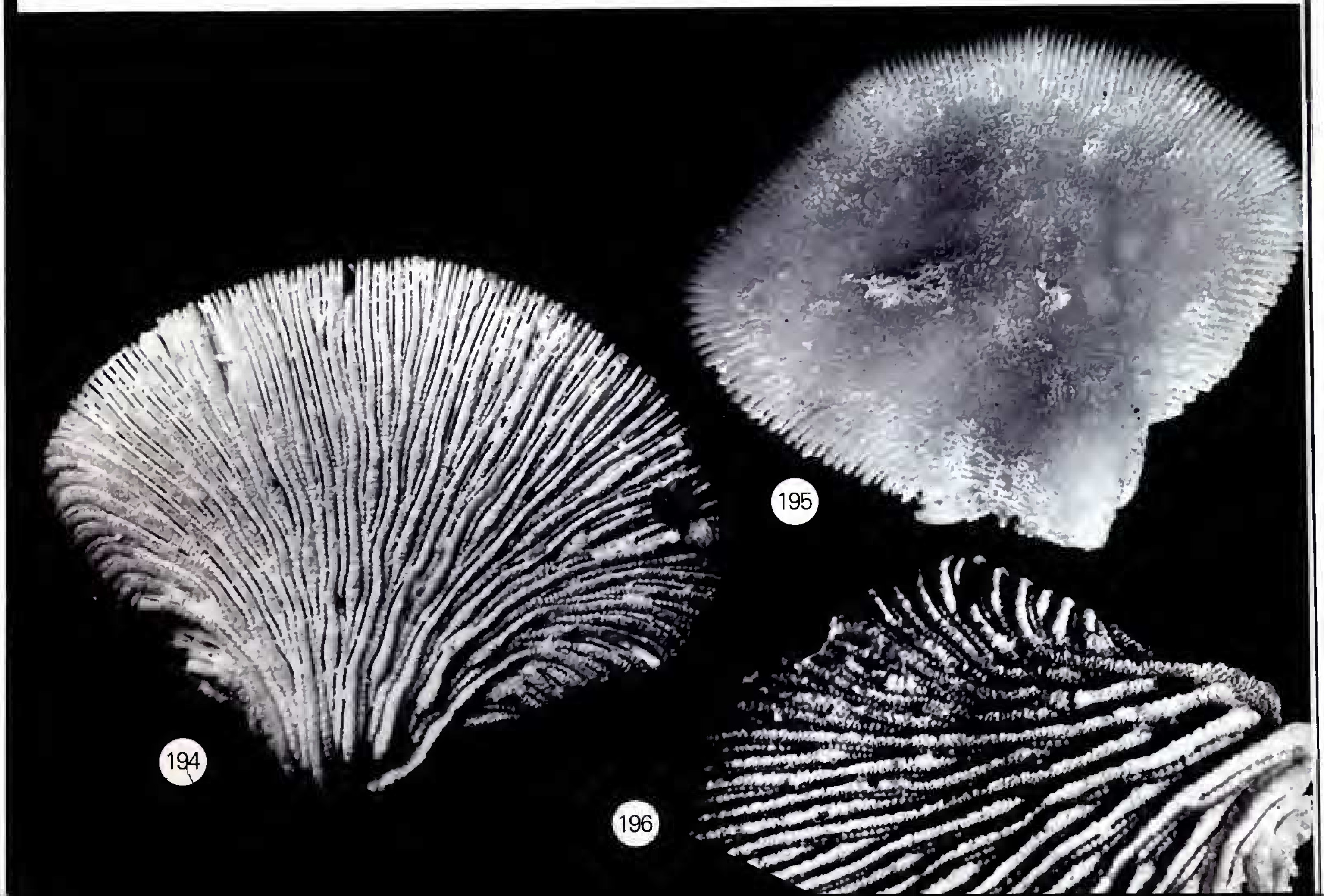
Septa are thick, close to each other, sometimes slightly wavy. Those of the lower orders are equal or are slightly arched around the central fossa. Those of the higher orders decrease abruptly in height, at the point where they fuse with two septa of a next higher order. Thus septa distinctly alternate in height towards the central part of the corallum. Just outside the point of fusion the high order septa are thickened and slightly arched in a manner similar to the tentacular lobes of some *Fungia* species. Septal margins bear numerous, small, triangular dentations, or bear granules which are either single and rounded or compound and hirsute. Septal sides, especially their lower part, are strongly granulated (Fig. 196). Columellae are papillose. Costae are numerous, narrow, close to each other, low and rounded. They decrease in size from the perimeter and may be $\frac{1}{4}$ the length of the radius or extend to the centre. They bear a row of minute conical spines, which lose their linear arrangement when the costae disappear in the central part of the corallum.

In the Great Barrier Reef, *D. distorta* is apparently restricted to soft substrates under the influence of currents, including tidal currents.

Affinities

The affinities of *D. distorta* with *D. fragilis* are discussed with the latter species (p. 123). It has uncertain affinities with *D. pulchella* Verrill, from Japan which is mentioned neither by Döderlein (1902) nor by Yabe & Sugiyama (1941). Vaughan's (1907) tabular description of the macroscopic structures of *Diaseris* suggests that it is close to *D. distorta*, but this requires further investigation.

Figs. 194-196 *Diaseris distorta* from Lizard Island (× 4.0). Figs. 194, 195, same corallum.



Distribution

Recorded from the Red Sea, Zanzibar, Madagascar, Aldabra, the Maldive Islands, Sri Lanka, Indonesia, the Philippines and the Great Barrier Reef.

Diaseris fragilis Alcock, 1893

Synonymy

Cycloseris freycineti (Edwards & Haime); *sensu* Quelch (1886).

Diaseris fragilis Alcock, 1893.

Fungia fragilis (Alcock); Vaughan (1907); Gardiner (1909); Boschma (1923b, 1925).

Fungia patella (Ellis & Solander); (*pars*) Döderlein (1902); (*pars*) van der Horst (1921).

Cycloseris fragilis (Alcock); Wells (1954); *non* Maragos (1977).

Material studied

Murray Islands (3 specimens), **Lizard Island** (18 specimens), **Bowl Reef** (18 specimens), **Palm Islands** (3 specimens), **Whitsunday Islands** (3 specimens), **Gould Reef, Bushy Island-Redbill Reef, Pompey Complex** (7 specimens), **Swain Reefs** (3 specimens).

These localities include collecting stations 75, 79, 80, 97, 113.

Previous records from Eastern Australia

Not previously recorded.

Characters

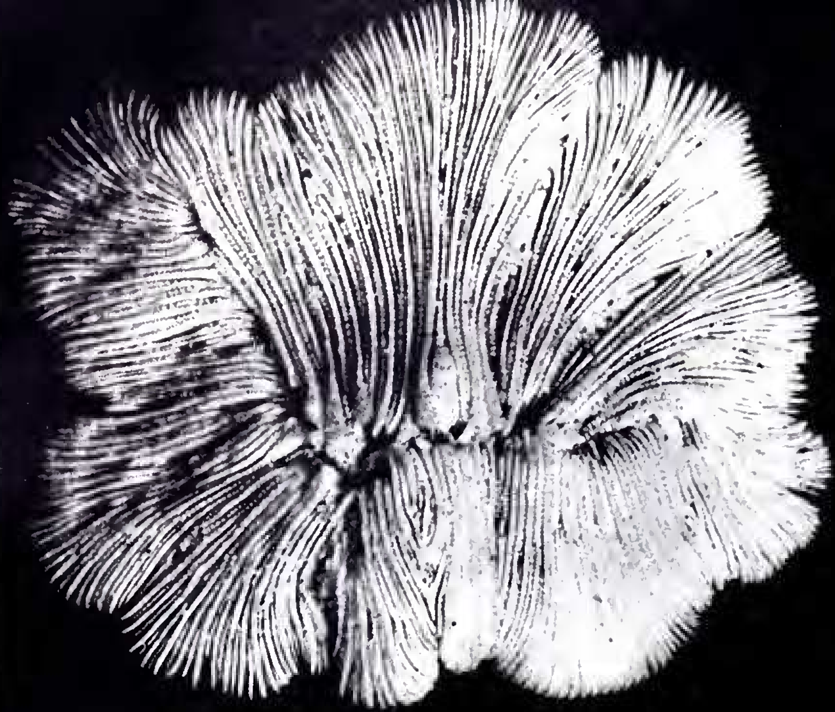
Coralla are up to 7 cm diameter, irregularly circular in outline, generally composed of several wedge-shaped sectors which break apart as a means of reproduction. The separation between the various sectors (six in number in complete, young coralla) does not necessarily bear any relationship to the first cycle of septa. Each sector, when becoming isolated, can regenerate an entire, more or less circular corallum. This process, however, is irregular and some adult colonies may develop several columellar centres. Coralla are flat, the undersurface is horizontal, the upper surface is very slightly elevated towards the centre. Coralla have a comparatively thin periphery, gradually increasing in thickness towards the centre.

Septa are numerous, thick, close to each other and slightly alternating in size and thickness. They maintain their relative heights from the corallum periphery to the centre, and higher order septa do not abruptly decrease in height when they fuse with septa of the next higher order as they do in *D. distorta.* Septal margins bear small, triangular dentations, or thick, irregular or rounded granules. They can be laciniate and ragged, with pillar-like dentations covered with granules. Septal sides are strongly granulated, with many perforations in the upper part. Synapticulae are usually visible from above in some parts of the corallum.

Costae are numerous, rounded, close to each other, becoming lower and then disappearing towards the corallum centre. They bear numerous, regular, very small conical spines. In some coralla, groups of costae are separated by a narrow groove which may be perforated or replaced by a narrow incision extending from the corallum perimeter inward half the radius or more, and coralla tend to split along these grooves. *Diaseris fragilis* is found on a wide variety of reefal to soft, sandy substrates. They are grey-yellow to beige in colour, often with a pale green margin.

Affinities

Diaseris fragilis can be separated from *D. distorta* by its larger size, thinner



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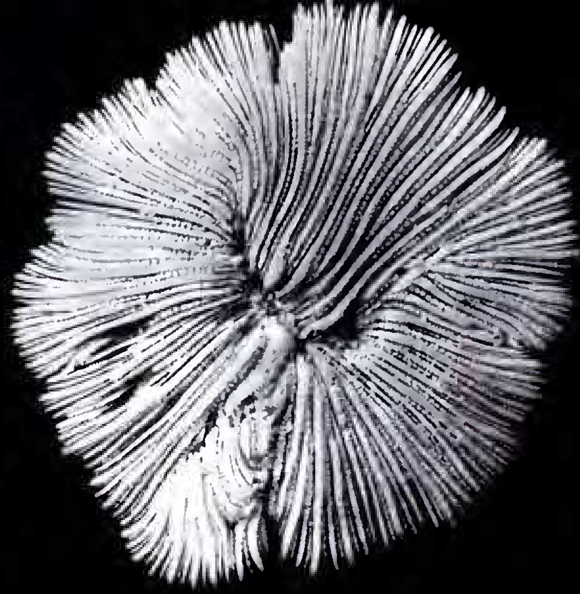

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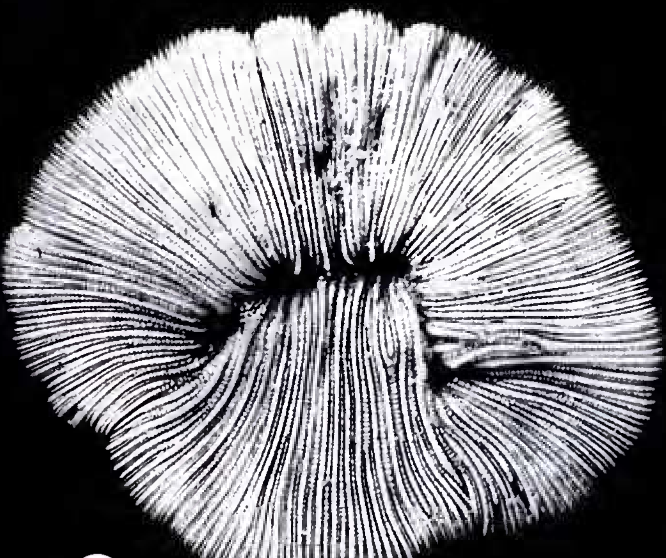

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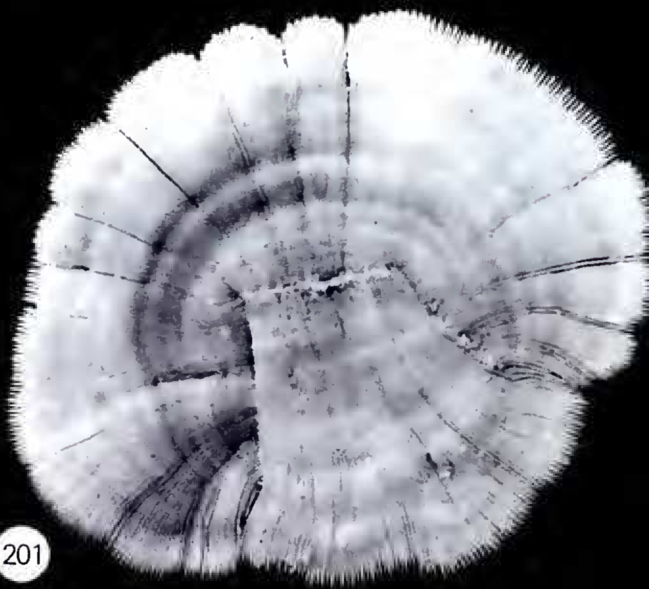


201

margins, and by the uniform height of the septa from the margins to the centre of the corallum.

Cycloseris discus Quelch, 1886 (also recorded as *Fungia discus* by Faustino, 1927) also has some characters in common with *D. fragilis*. Quelch's description is, however, insufficient to decide if the two species are identical or not.

Distribution

Recorded from the Seychelles Islands, the Andaman Sea, Indonesia, the Philippines, the Great Barrier Reef, the Marshall Islands and Hawaii.

GENUS *HELIOFUNGIA* WELLS, 1966

Type species *Fungia actiniformis* Quoy & Gaimard, 1833.

Affinities

Heliofungia was established as a subgenus of *Fungia* by Wells (1966), along with *Verrillofungia, Danafungia* and Verrill's older names *Pleuractis* and *Ctenactis.*

Apart from its characteristic skeletal structures, *Heliofungia* is readily distinguished from other *Fungia* subgenera by its large polyps with long, continually extended tentacles (Fig. 202, 754). On these grounds, it seems justified, as already suggested by Döderlein (1902) and more recently by Wells (1966), to consider *Heliofungia* as a separate genus rather than a subgenus of *Fungia. Heliofungia* is therefore raised to the rank of genus, including only one species, *H. actiniformis.*

Heliofungia has been recorded from the Miocene of Indonesia, and appears to be an early offshoot from the evolutionary sequence of *Fungia.*

Heliofungia actiniformis (Quoy & Gaimard, 1833)

Synonymy

Fungia actiniformis Quoy & Gaimard, 1833; Edwards & Haime (1851a, 1860); Studer (1877); Döderlein (1902); Bedot (1907); van der Horst (1921); Boschma (1923a, 1925); Faustino (1927); Thiel (1932); Eguchi (1938); Yabe & Sugiyama (1941); Nemenzo (1955a); Searle (1956); Rossi (1956); Wells (1956).

Fungia crassitentaculata Quoy & Gaimard, 1833; Edwards & Haime (1851a, 1860); Ortmann (1888); Rehberg (1892); Saville-Kent (1893); ? Gardiner (1898).

Fungia diversidens Edwards & Haime, 1851a; Edwards & Haime (1860).

Material studied

Big Mary Reef, Turtle Backed Island, Thursday Island, Yorke Island, Tijou Reef, Low Isles, Palm Islands (21 specimens), **Pandora Reef** (2 specimens), **Whitsunday Islands** (3 specimens), **Swain Reefs** (2 specimens).

These localities include collecting stations 6, 12, 13, 34, 35, 38, 41, 43, 45, 57, 67, 79, 92, 97, 98, 111, 131, 137, 138.

Figs. 197-201 *Diaseris fragilis* (× 2.0).

Figs. 197, 200 Same corallum from Gould Reef, collecting station 113.
Fig. 198 From the Pompey Complex, collecting station 75.
Figs. 199, 201 Same corallum from the Swain Reefs, collecting station 79.

Previous records from Eastern Australia

Low Isles, Yonge (1930), Stephenson *et al.* (1931), Marshall & Orr (1931), Yonge, Yonge & Nicholls (1932), Yonge (1940), Crossland (1952), Stephenson & Wells (1955).

Characters

Coralla are circular or slightly oval, thick and heavy, up to 20 cm diameter and up to 7 cm high. Septa of the first three or four orders are prominent, with coarse, triangular or (commonly) lobate dentations, up to 5-7 mm in length with minutely serrated margins. Septa of the higher orders have smaller, less conspicuous, more rounded and lobulate dentations than those of the lower orders. All septa are granulated. Coralla margins are relatively thick. Undersurfaces have a distinct scar of attachment, even in adult stages. They are imperforate or, exceptionally, show only a few elongate pits in the marginal part. Costae are numerous, equal or subequal and extend to the centre of the corallum, except for those corresponding to the very high orders which are only developed in the margins. Costae are laminar ridges, uniform towards the periphery of the corallum, becoming irregular towards the centre. Their free margins are scalloped or bear low, rounded or subtriangular, blunt dentations.

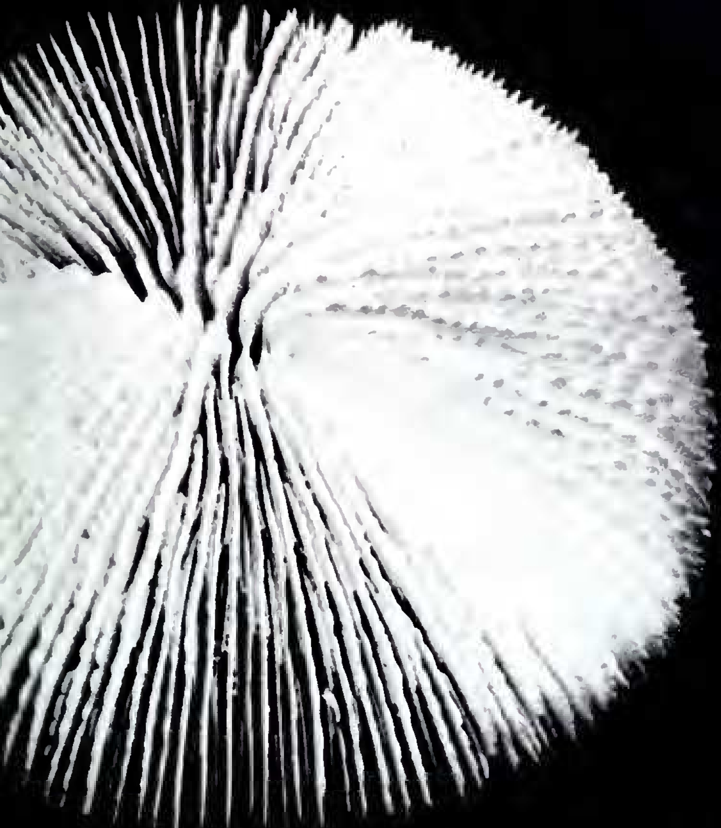
Polyps are almost always fully expanded, projecting largely above and around the corallum, with numerous thick tentacles up to 8 cm long, bearing a well defined terminal knob.

Fig. 202 *Heliofungia actiniformis* from the Swain Reefs showing tentacles expanded.

Figs. 203-205 *Heliofungia actiniformis* (× 1.0).

Figs. 203, 204 Same corallum, from the Swain Reefs, collecting station 67.
Fig. 205 From Tijou Reef, collecting station 6.

Fig. 202 ▼



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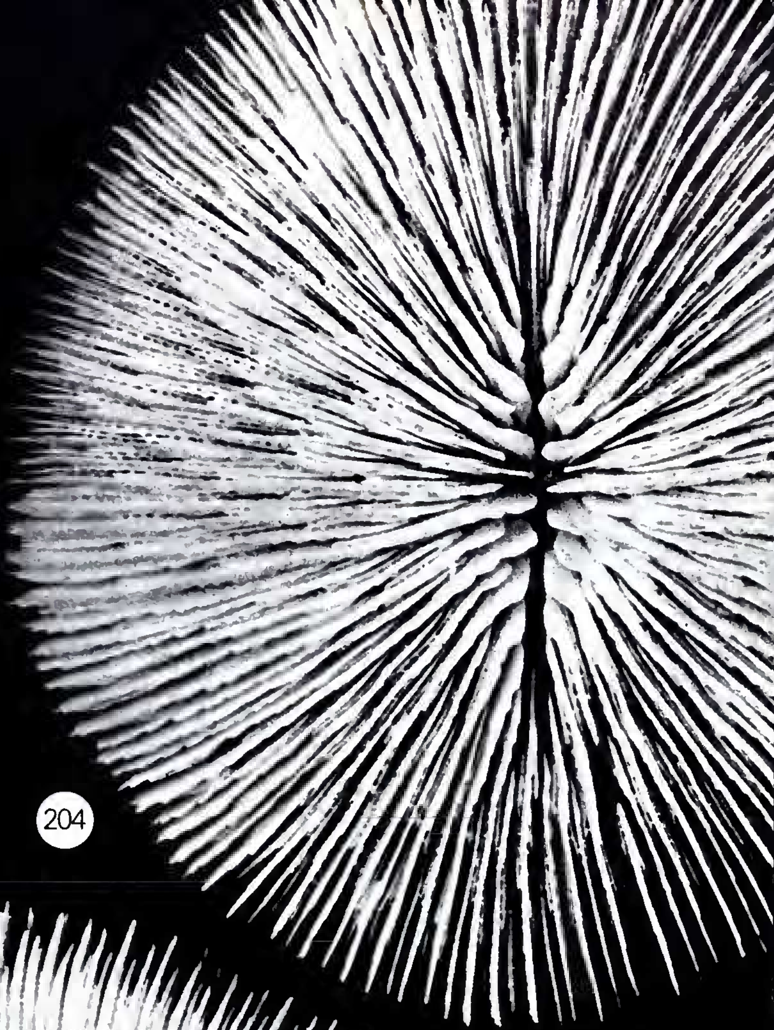

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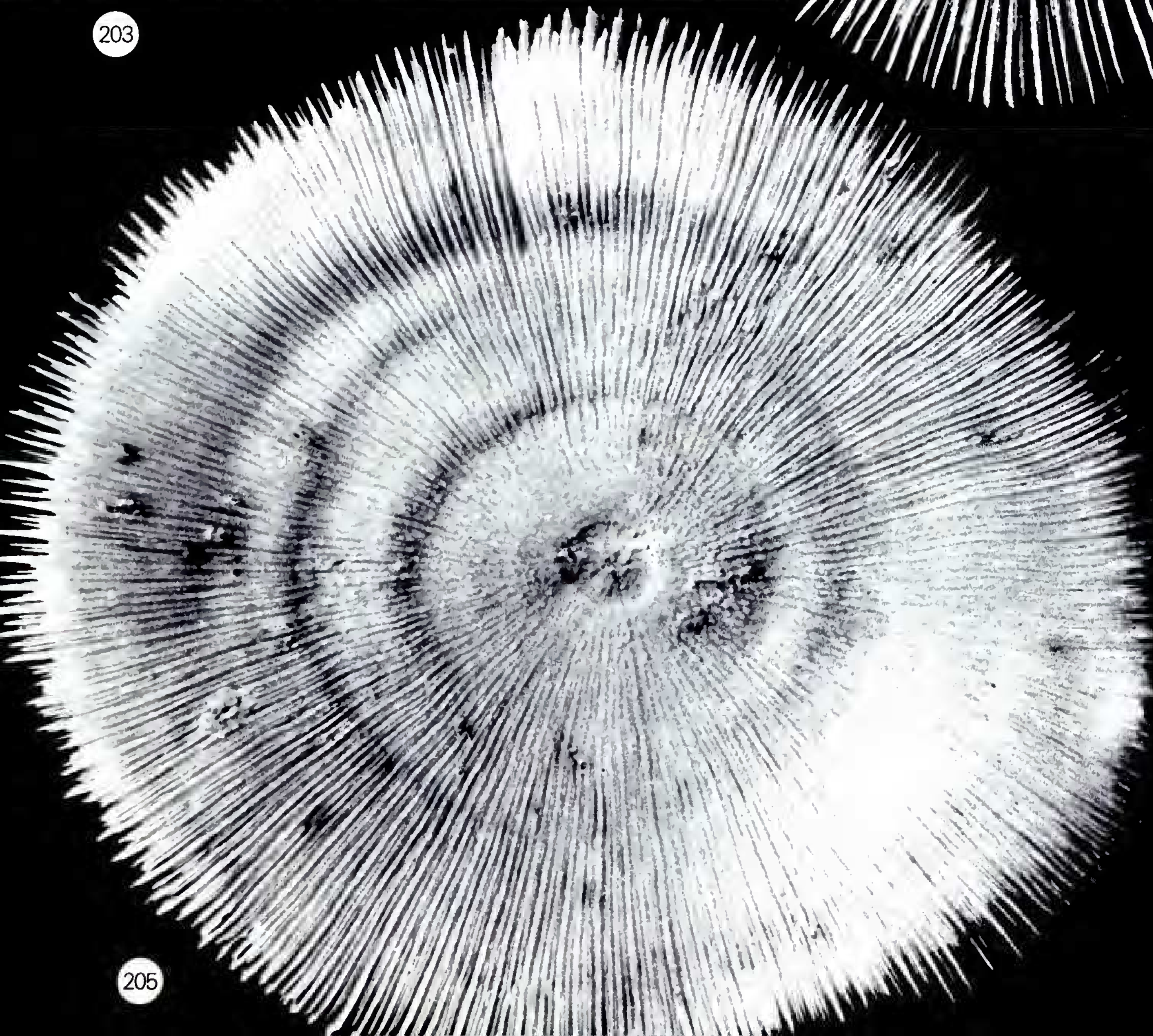

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Skeletal variations

Döderlein (1902) described 5 varieties of *H. actiniformis*, one being the nominal species *crassitentaculata* of former authors. Most of the present series (which have a triangular rather than lobate ornamentation of the septal margin) correspond to Döderlein's variety *paulawensis*. These varieties, however, are based on only minor differences in the morphology and ornamentation of the septa and costae and some were established on one or a small number of specimens. The present series indicates that there is continuous variation between Döderlein's varieties and thus infraspecific taxa are not separated. This position is in agreement with Rossi's (1956) general conclusion that it is not possible to recognise and define polytypic conditions in *Fungia* species.

Distribution

Recorded from the Indian Ocean (Cocos-Keeling Islands) and the western Pacific: Malaya, Singapore, Indonesia, New Guinea, Philippines, Palau, New Caledonia, New Hebrides and the Great Barrier Reef. Gardiner's (1898) record of *F. crassitentaculata* from Rotuma is doubtful.

GENUS *FUNGIA* LAMARCK, 1801

Generic synonymy

Fungia Lamarck, 1801.

Haliglossa Ehrenberg, 1834 (*pars*).

Ctenactis Verrill, 1864.

Lobactis Verrill, 1864.

Pleuractis Verrill, 1864.

Type species *Madrepora fungites* Linnaeus, 1758.

Characters of the genus (after Wells, 1966)

Coralla are free, solitary (monostomodaeal), discoid or elongate-oval, flat or convex. The wall is perforate in juvenile stages with perforations still present in adult stages of some species. Septa are generally imperforate, except for higher orders. Septal dentations are large, rounded, subtriangular or triangular. Costae are mostly reduced to rows of spines.

Introduction

Species of *Fungia* fall into natural, homogeneous groups. Subdivision of the genus was initiated by Verrill (1864) who removed from *Fungia* proper all species with an oval-elongate corallum and divided them into the separate genera *Ctenactis, Pleuractis* and *Lobactis*. Later, Döderlein (1902) divided *Fungia* into 6 groups primarily on the basis of the shape of the corallum and also of the nature of septal dentations and costal structures. These were subsequently recognised by Wells (1966) as subgenera. Two of these subgenera were given Verrill's names and *Lobactis* was synonymised with *Pleuractis* and, in addition to the nominate subgenus *Fungia*, the names *Danafungia, Verrillofungia* and *Heliofungia* were established for the 3 remaining groups. The correspondence between Döderlein's groups and Wells' subgenera are:

actiniformis group	:	subgenus *Heliofungia*
scutaria group	:	subgenus *Pleuractis*
echinata group	:	subgenus *Ctenactis*
repanda group	:	subgenus *Verrillofungia*

danai group : subgenus *Danafungia*
fungites group : subgenus *Fungia*

In the present study, the subgenus *Heliofungia* is raised to a generic rank (see p. 125), and Wells' 5 remaining subgenera are used without further change.

Gardiner (1909) listed 22 species which can be referred to one of these 5 subgenera and since then there have been few changes. One species, *F. oahensis*, is synonymous with *F. scutaria* but only three or four valid new species have subsequently been described. Out of the 25 or so species presently referred to *Fungia*, 15 are now known from the Great Barrier Reef.

Subgenus *Fungia* Lamarck 1801

The subgenus *Fungia* is characterised by a discoidal corallum with septal dentations basically triangular and often of large size. Costal spines are tall and conical, either entirely smooth or with smooth sides and spinulose tips, awl-like towards the corallum perimeter.

The subgenus includes one very abundant and extremely polymorphic species, described by older authors under at least 8 different names in which Döderlein (1902) separated 13 varieties.

Vaughan (1906b) stated that the affinities of his *Fungia madagascariensis* are with *F. fungites*, but the present study indicates that it is more likely to belong to the subgenus *Danafungia*.

Fungia (Fungia) Fungites (Linnaeus, 1758)

Synonymy (partly after Döderlein, 1902)

Madrepora fungites Linnaeus, 1758; Forskål (1775); Ellis & Solander (1786); Esper (1791).

Madrepora echinata Esper, 1791.

Fungia agariciformis Lamarck, 1801; Lamarck (1816); Lamouroux (1821); Stutchbury (1833); Ehrenberg (1834); Leuckart (1841).

Fungia discus Dana, 1846; Edwards & Haime (1851a, 1860); Quelch (1886); Studer (1877); Saville-Kent (1893).

Fungia dentata Dana, 1846; Verrill (1864); Quelch (1886); Ortmann (1888); Gardiner (1898); Studer (1901).

Fungia confertifolia Dana, 1846; Edwards & Haime (1851a, 1860); Verrill (1864); Brüggemann (1879b); Quelch (1886); Ortmann (1888).

Fungia patellaris Edwards & Haime, 1848; Gardiner (1899b).

Fungia patella Edwards & Haime, 1851a; Edwards & Haime (1860); Klunzinger (1879); Gardiner (1898).

Fungia tenuifolia Edwards & Haime, 1851a; Edwards & Haime (1860).

Fungia crassilamellata Edwards & Haime, 1851a; Edwards & Haime (1860).

Fungia haimei Verrill, 1864; Brüggemann (1879a); Studer (1901).

Fungia papillosa Verrill, 1868; Brüggemann (1879b); Rehberg (1892).

Fungia lacera Verrill, 1868; Saville-Kent (1893).

Fungia pliculosa Studer, 1877.

Fungia fungites (Linnaeus); Döderlein (1902); Gardiner (1905, 1909); von Marenzeller (1907); Vaughan (1907b, 1918); Harrison & Poole (1909a); Gravier (1907, 1911); van der Horst (1921); Boschma (1923a, 1925, 1929); Matthai (1924); Hoffmeister (1925); Faustino (1924); Thiel (1932); Eguchi (1938); Umbgrove

(1939, 1940); Yabe & Sugiyama (1935, 1941); Crossland (1952); Rossi (1954, 1956); Wells (1954, 1966b); Nemenzo (1955a); Stephenson & Wells (1955); Searle (1956); Ma (1959); Pichon (1964); Scheer (1967); Rosen (1971); Pillai & Scheer (1973, 1974); Scheer & Pillai (1974); Zou (1975a); Pillai & Scheer (1976).

Material studied

Bramble Cay, Pearce Cay (2 specimens), **Yorke Island, Murray Island** (5 specimens), **Turtle Backed Island** (3 specimens), **Dungeness Island** (7 specimens), **Jervis Reef** (4 specimens), **Wai Weer Island, Ashmore Reef** (2 specimens), **Sue Islet, Northwest Reef, Great Detached Reef** (2 specimens), **Tijou Reef** (2 specimens), **Bewick Island** (2 specimens), **Jewell Reef** (4 specimens), **Lizard Island** (8 specimens), **Waining Reef, Ribbon Reef** (6 specimens), **Hope Island** (2 specimens), **Old Reef, Gould Reef, Palm Islands** (28 specimens), **Rattlesnake Island, Whitsunday Islands** (7 specimens), **Pompey Complex** (3 specimens), **Swain Reefs** (3 specimens), **Frigate Cay, Heron Islands** (3 specimens).

These localities include collecting stations 1, 2, 11, 13, 14, 17, 18, 27, 30, 32, 34, 35, 37, 39, 41, 56, 57, 58, 60, 61, 62, 63, 64, 67, 71, 75, 77, 79, 81, 93, 94, 96, 98, 99, 100, 102, 105, 106, 109, 114, 115, 116, 119, 122, 124, 128, 130, 135, 138.

Previous records from Eastern Australia

Murray Islands, Vaughan (1918); **Low Isles,** Stephenson & Stephenson (1933), Crossland (1952), Stephenson & Wells (1955); **Heron Island,** Salter (1954).

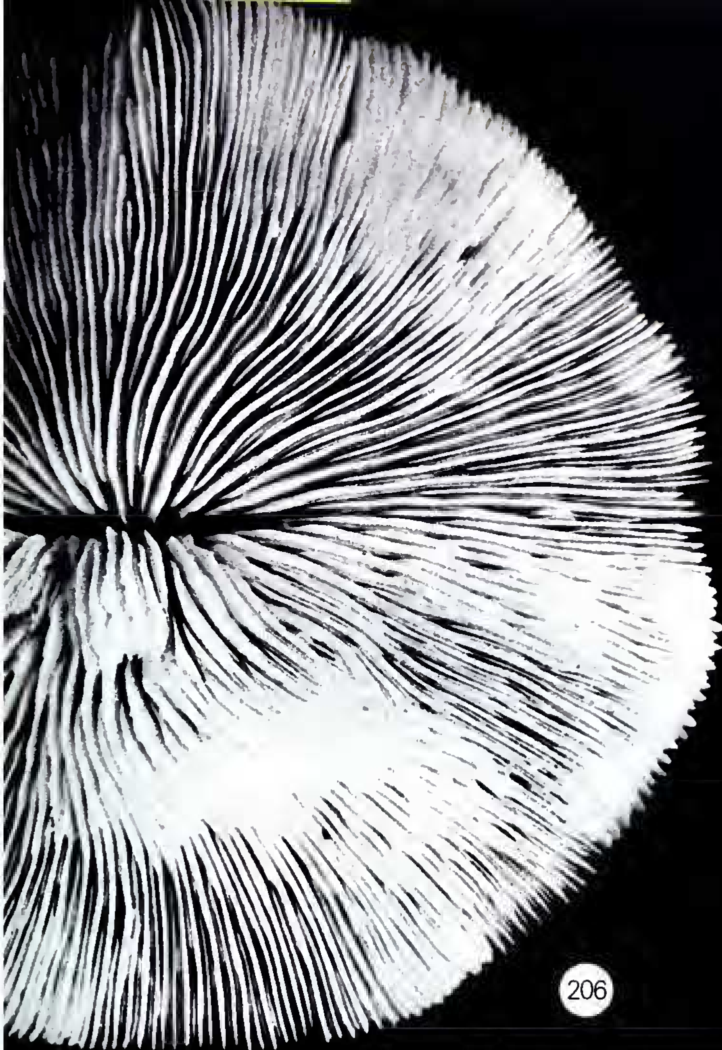
Characters and skeletal variations

Coralla are circular or slightly oval, regular or irregular in outline and up to 28 cm diameter. They are mostly flat or slightly convex, with a uniform thickness. Only a few specimens have the disc conspicuously arched.

Septa are numerous, close to each other, equal or subequal, comparatively thin, sometimes slightly wavy in outline (Fig. 208). Dentations vary greatly in shape and ornamentation; usually they are triangular and slightly thickened in a trabecular direction at the apex. Septal margins may be almost totally devoid of any ornamentation, although they are somewhat irregular. The shape of the dentations varies from obtuse (low triangular or lobate) to acute. In some instances (as in Döderlein's varieties *stylifera* or *columnifera*) the dentations become high and irregular, composed of tall, narrow lobes (var. *columnifera*) or with styloid tips (var. *stylifera*) curving in various directions. In some specimens a weak tentacular lobe is present on secondary septa. The mouth fossa is very elongate and narrow, particularly in larger specimens. The columella is composed of papillae fusing with the lower and inner part of the principal septa. Costae are equal or subequal, numerous and are ornamented with spines which are typically conical, with smooth, even sides and spinulose tips. They have a wide range of sizes; in some specimens they are less than 1 mm high, and in others (Döderlein's varieties *dentata* and *stylifera*) they can be as much as 4 mm high. The basal diameter to height ratio of the spines is also very variable, although this criterion was used by Döderlein to establish some of his varieties. Specimens with tall, thick costal spines (e.g. Döderlein's variety *dentata*), superficially resemble some species of *Danafungia*, in particular *F. danai*, hence the confusion made by some authors. The number of spines on the costae is also highly variable, from few scattered spines, to an undersurface entirely covered by densely packed spines. The wall can be very perforate (almost to the centre of the disc) or solid.

Figs. 206-209 *Fungia fungites* upper surface (× 1.0).

Figs. 206, 209 From between Orpheus and Fantome Islands, Palm Islands, collecting station 60.
Fig. 207 From Lizard Island, collecting station 32.
Fig. 208 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.



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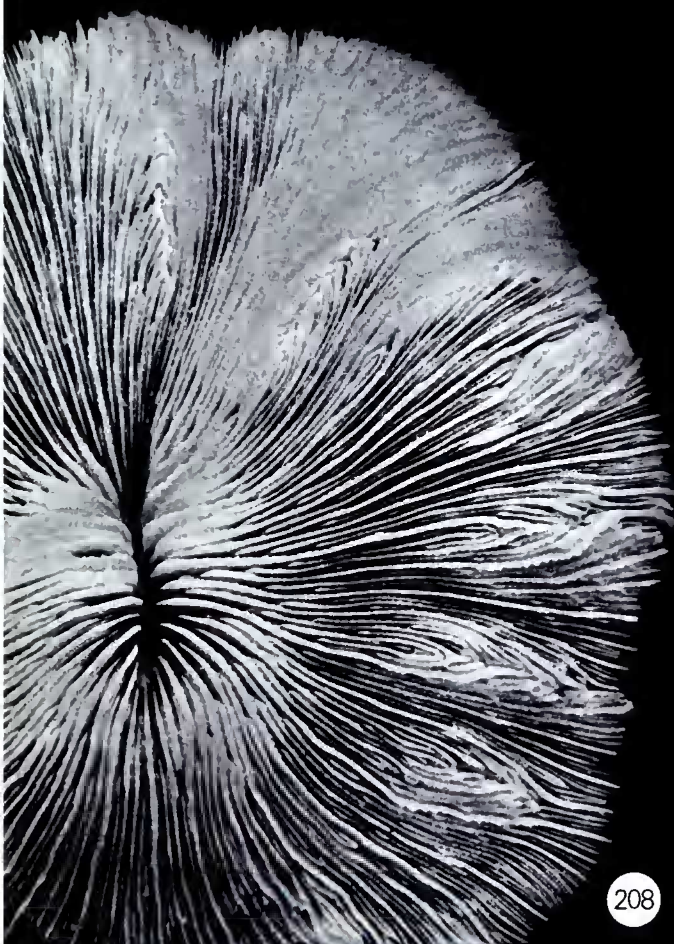

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Affinities

Despite its enormous variability, *F. fungites* is a well characterised species and its identification usually raises few problems. Its variability led a number of early authors to consider as distinct species what are only several instances of intraspecific variations. Döderlein (1902) typified 13 varieties within *F. fungites* to which two others were recently added by Nemenzo. The status of these 'varieties', as infraspecific biological taxa, is unclear: they are neither ecomorphs nor geographical subspecies. Several can be found together, not only in the same geographic region, but in the same sampling station. However, in any given region, one variety is usually dominant over the others, e.g. Wells (1954) found *Fungia fungites haimei* dominant in the Marshall Islands whilst Rossi (1956) found *Fungia fungites agariciformis* dominant in Red Sea. Döderlein's varieties are also of limited interest because of the existence of intermediate forms. This was actually recognised by Döderlein himself who, in several instances, was led to use two variety names for single specimens—*F. fungites* var. *dentata-papillosa, F. fungites* var. *stylifera-confertifolia, F. fungites* var. *confertifolia-columnifera* and *F. fungites* var. *stylifera-haimei.*

In the field, *F. fungites* has often been confused with some species of *Danafungia*, in particular *F. danai*, but the distinction between the two in laboratory does not raise any special difficulty. (see p. 132).

Distribution

Widely distributed throughout the Indo-Pacific.

SUBGENUS *DANAFUNGIA* WELLS, 1966

The subgenus *Danafungia* was established by Wells, for species of the *'danai'* group discussed by Döderlein.

The skeletal characteristics of *Danafungia*, as defined by Wells are as follows:

(1) Large, lobulate septal dentations, each composed of a fan system of trabeculae diverging radially and emerging laterally as small spines.

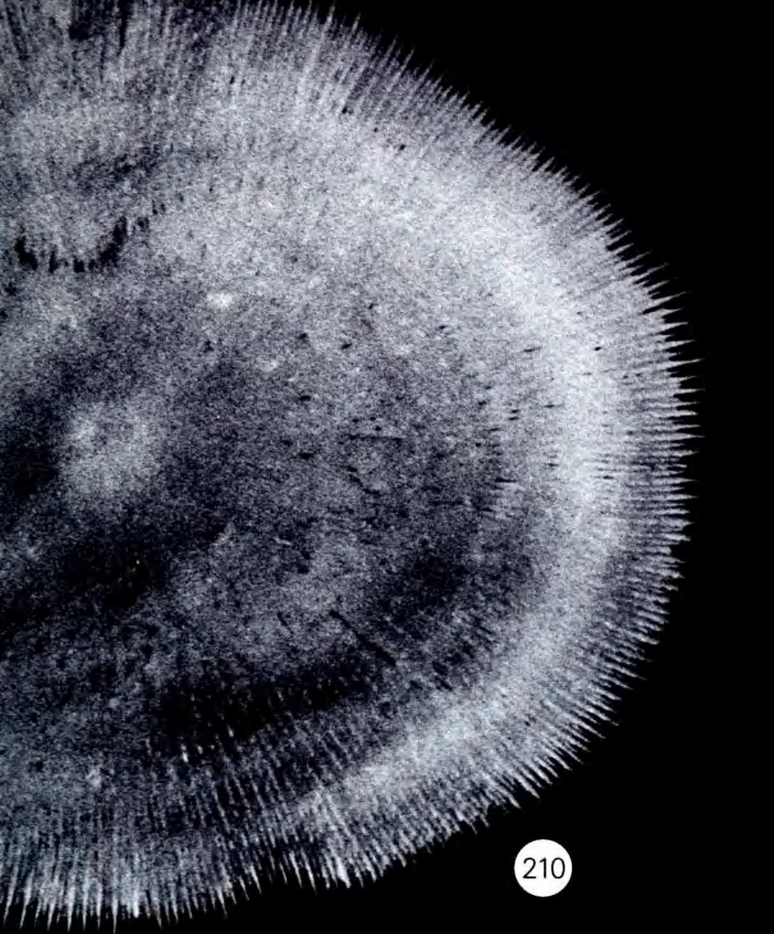
(2) Only the lower cycle costae bearing long, blunt, spinulose spines, the higher cycle costae generally spineless, the centre of the aboral surface only sparsely spined.

These characters are quite distinctive and thus *Danafungia* is an easily identified subgenus. The only area of confusion may be with the very hirsute or spinose forms of *Fungia fungites*, such as Döderlein's varieties *confertifolia, stylifera* and *dentata.* The nature of costal spinulation, however, remains quite distinct in the two subgenera.

Döderlein included eight species in his *'danai'* group. Whereas the distinctions between the four species with a perforate wall (*danai, scruposa, corona, subrepanda*) remain clear, the differences between the species with an imperforate wall are less obvious, in particular in the *valida/horrida/acutidens* series. This problem could not be investigated in detail in the present study as *F. valida* is very rare and *F. acutidens* is apparently absent from eastern Australia. From the examination of material from

Figs. 210-213 *Fungia fungites* undersurface (× 1.0).

Fig. 210 From Frigate Cay, collecting station 81.
Fig. 211 From Fantome Island, Palm Islands, collecting station 34.
Fig. 212 From between Orpheus and Fantome Islands, Palm Islands, collecting station 60.
Fig. 213 From Lizard Island.



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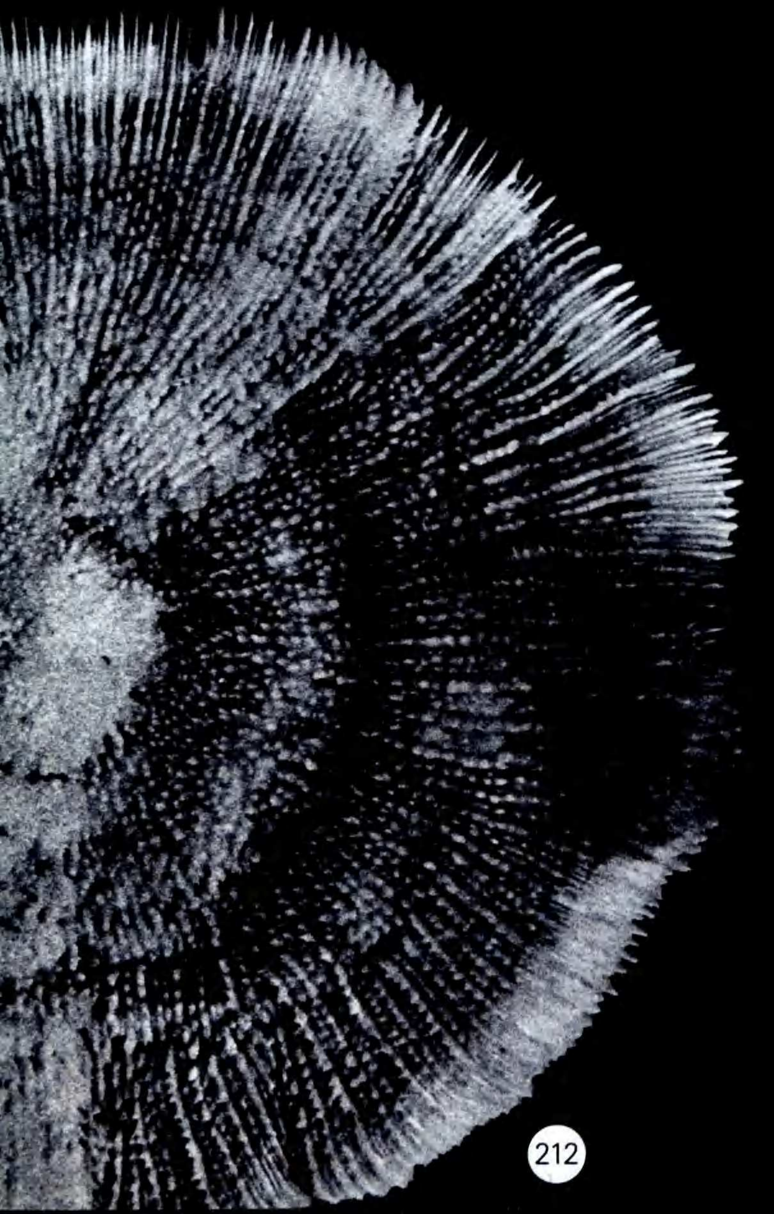

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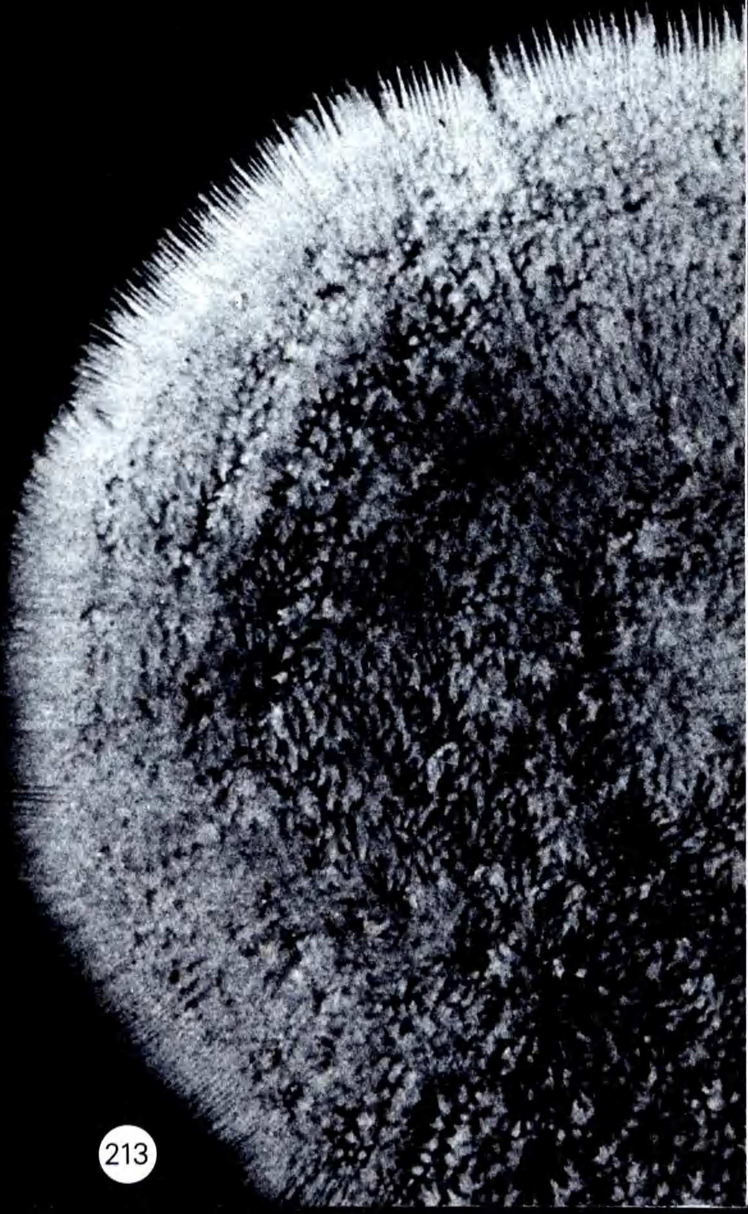

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various other Indo-Pacific regions it appears that *F. valida, F. horrida* and *F. klunzingeri*, at least, stand as separate species, even if the distinction between them is not always clear.

Other species possibly belonging to the subgenus *Danafungia* described since Döderlein are *F. madagascariensis* Vaughan, and *F. fieldi* Gardiner. The status of these two species, which come very close to each other, has not been further studied.

The affinities of *F. fralinae* Nemenzo remain doubtful as the original description and figures are unclear. Although Nemenzo described *F. fralinae* with *F. danai* and *F. horrida*, the 'very finely serrate' septal margin throws doubt on its inclusion in *Danafungia*.

Fungia (Danafungia) danai Edwards & Haime, 1851

Synonymy

Fungia danai Edwards & Haime, 1851a; Edwards & Haime (1860); Verrill (1864); Semper (1872); Studer (1880); Ortmann (1889); Döderlein (1902); Gardiner (1905, 1909); van der Horst (1921); Matthai (1924); Boschma (1925, 1929); Faustino (1927); Thiel (1932); Yabe & Sugiyama (1935, 1941); Umbgrove (1939, 1940); Nemenzo (1955a); Wells (1966); Pillai & Scheer (1976).

Fungia echinata Dana (1846).

Fungia dentata Edwards & Haime, 1851a; Edwards & Haime (1860).

Fungia lobulata Ortmann, 1889.

Material studied

Bramble Cay, Darnley Island (2 specimens), **Yorke Island** (5 specimens), **Murray Island** (2 specimens), **Lizard Island** (3 specimens), **MacGillivray Reef, Ribbon Reef** (4 specimens), **Low Isles** (2 specimens), **Palm Islands** (5 specimens), **Gould Reef, Bushy Island-Redbill Reef, Pompey Complex, Swain Reefs.**

These localities include collecting stations 12, 13, 27, 32, 34, 41, 42, 63, 65, 69, 71, 74, 80, 92, 99, 114, 128, 130.

Previous records from Eastern Australia

Not previously recorded. The name *Fungia danai* as used by Yonge *et al.* (1932) refers to *Fungia fungites*, according to Stephenson & Wells (1955).

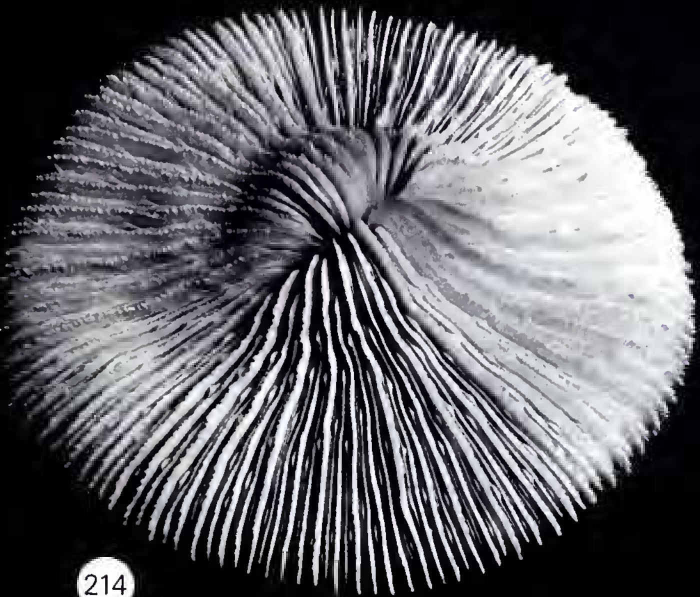
Characters

Coralla are irregularly circular and may reach a large size (up to 29.5 cm diameter). They are flat or conspicuously arched, with most specimens having an irregularly concave undersurface and convex oral surface, the central part of which is arched around the central fossa.

Septa of the first three orders are markedly more exsert than those of the higher orders, both at the corallum periphery (Fig. 217) and at the central fossa. The margins of the higher orders bear irregular, subtriangular dentations, the tips of which are either rounded or pointed. The central axes of the dentations are thickened in a rod of trabecular direction, which produces irregular ridges or hillocks on the sides of the dentations. The lower parts of the septa are covered with small spines. Margins of

Figs. 214-217 *Fungia danai*

Fig. 214	From Esk Island, Palm Islands, collecting station 42. (× 0.5).
Fig. 215, 217	From Great Palm Island, collecting station 92. (× 0·8, 2·0)
Fig. 216	From Yorke Island, collecting station 13. (× 0·8)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higher orders bear the same type of dentations (although smaller and more regular) as those of the lower orders. Tentacular lobes are often present. In some specimens, synapticulae are distinctly visible between the septa. The central fossa is elongate; the columella spongy.

Costae are very unequal. Only those of the lower orders bear spines. Those of the higher orders, which can be distinctly followed to half the disc radius, are smooth and rounded. Spines of the lower costae are tall, subcylindrical or conical, simple or arborescent, bifurcating, or branching in all directions (Fig. 215). In some specimens, costal spines tend to be slightly compressed radially, but never to the extent of *F. corona.* Spines are spinulose at their tips and their sides are covered with small, rounded, irregular granules or blunt spinules. They occur almost to the centre of the corallum. Walls have numerous perforations. Towards the margins of the corallum, perforations appear as long narrow slots, originating from the incomplete fusion of costae. Towards the centre of the corallum, perforations (which are to be found over the whole undersurface, except the very centre) are still slightly elongate, but tend to become isodimensional.

Affinities

Fungia danai is characterised by its very exsert septa of lower orders and by its coarse, hirsute costal spines. In the field it resembles *F. horrida,* but the latter does not have a perforate wall, and its septal dentations are more irregular. *Fungia scruposa* also shows some affinities with *F. danai,* particularly when the latter has irregular, thickened septal dentations. It is unlikely, however, that the two species can be confused.

As previously mentioned, *F. fungites,* particularly its most coarsely spinose forms, has been previously misidentified as *F. danai.* This is largely because insufficient attention has been paid to the structures and ornamentations of the septal dentations and costal spines, the importance of which has only recently been stressed (Vaughan & Wells, 1943; Wells, 1956, 1966). However, where *F. danai* has almost smooth-sided costal spines, and *F. fungites* spinulose costal spines, they can be distinguished by other characters, especially *F. danai's* exsert lower orders of septa and smooth secondary costae.

The relationships of *F. madagascariensis* Vaughan (1905) are more ambiguous. Despite Vaughan's claim that his species is nearest to *F. fungites* var. *dentata,* the type specimen has affinities with the subgenus *Danafungia,* particularly with *F. danai.* Vaughan himself noted that *F. madagascariensis* differs from *F. fungites* var. *dentata* 'especially in the character of the spines'.

Distribution

Apparently not recorded from the Red Sea, but otherwise widespread in the tropical Indo-pacific from Madagascar to Tahiti and the Tuamotu Archipelago.

Fungia (Danafungia) corona Döderlein, 1901

Synonymy

Fungia corona Döderlein, 1901; Döderlein (1902); Gardiner (1909); Matthai (1924).

Material studied

Yorke Island, Palm Islands (2 specimens), **Frigate Cay.**
These localities include collecting stations 13, 36, 60, 81.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are basically circular, but irregular in outline, flat, or slightly and unevenly arched. Septa are markedly alternating in size, comparatively thin, those of lower orders being distinctly higher, from the margins to the centre. Septal dentations are irregular, triangular, often with pointed tips which appear thickened owing to the existence of well developed but irregular ridges running vertically, in a trabecular direction, to their tips. A tentacular lobe, which may be only weakly developed, is present on septa of higher orders. Synapticulae are visible between the septa. The central fossa is only slightly elongate, the columella small. Costae alternate in size towards the margins of the corallum. Those of lower orders appears to be laminar, particularly in their outer part. Costal spines are tall, comparatively few in number, but evenly distributed on the costae. Their tips are spinulose and their sides bear irregular, blunt, small, rounded spines or granules. They often are slightly compressed laterally, particularly in the peripheral part of the corallum. The undersurface has numerous, narrow, elongate perforations (Fig. 221).

Affinities

All specimens of the present series are lightly calcified and differ from Döderlein's description in that the septa are not thickened themselves; only the vertical axes of their dentations are. There is, however, good agreement between the present series and Döderlein's published figure of this species.

Both Döderlein (1902) and Gardiner (1909) pointed out the close affinity between *F. corona* and *F. danai* and Gardiner (1909) even suggested that *F. corona* could fall within the limits of variations of *F. danai.* Although Gardiner's suggestion remains a possibility, there is not sufficient evidence available to lump the two species, which are distinguished as follows:

(1) Crests and ridges of the dentations are more prominent in *F. corona.*
(2) *Fungia corona* has fewer costal spines, rarely branching, compressed laterally, with comparatively smooth sides.

These characters seem to be constant in the few specimens known from other geographic areas.

Distribution

Recorded from Chagos, the Andaman Islands, the Mergui Archipelago, Singapore and the Great Barrier Reef.

Fungia (Danafungia) scruposa Klunzinger, 1879

Synonymy

Fungia scruposa Klunzinger, 1879; Döderlein (1902); von Marenzeller (1907); van der Horst (1921); Matthai (1924); Yabe & Sugiyama (1935a, 1941); Rossi (1956).

Material studied

Bramble Cay (2 specimens), **Pearce Cay, Murray Islands** (2 specimens), **Great Detached Reef, Lizard Island, Ribbon Reef, Palm Islands** (3 specimens), **Pompey Complex** (2 specimens), **Frigate Cay** (2 specimens).

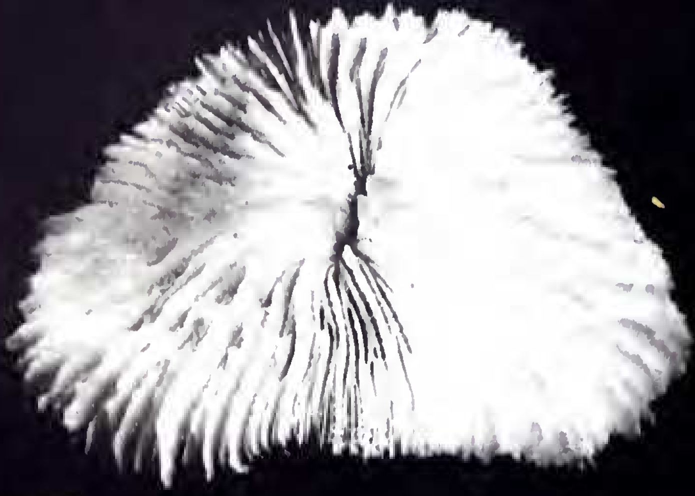
These localities include collecting stations 5, 11, 28, 34, 41, 56, 63, 71, 81, 124, 127, 128.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are circular or oval, almost flat or irregularly arched, comparatively thick



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and heavily calcified. The maximum diameter is 24 cm. In some specimens, the upper surface is slightly arched in its central part, around the axial fossa.

Septa are numerous, slightly unequal in the outer part of the corallum, but markedly unequal in the central part, where they are arched around the mouth fossa. Septa of lower orders are much thicker than those of the higher orders. Dentations of the septal margin are extremely irregular in size and shape; the basic type is irregularly triangular, but often the dentation tip extends in a thickened, vertical rod or in a knob-like projection. Dentations are also frequently of a styloid type, straight or curved; in the latter case the ends of neighbouring dentations can fuse, producing apertures along the septal margins. A tentacular lobe is occasionally present in septa of higher orders. The central fossa is elongate, the columellae weakly developed. The undersurface has numerous principal costae. Secondary costae, devoid of spines, are only visible at the corallum periphery. Costal spines which extend to the centre, are numerous, close to each other, tall and branch infrequently or are arborescent, with spinulose, hirsute tips. Their sides are covered with small, blunt spinules, rounded granules, or are almost smooth. The wall is very perforate, with perforations long and narrow towards the margins, more rounded towards the centre.

Skeletal variation

The shape of septal dentations is variable and usually in a given specimen one or two of the above-mentioned dentation types are dominant. Döderlein (1902) established the variety *ternatensis* for one specimen with regularly uniform triangular dentations and very hirsute costal spines. Some specimens of the present series show *ternatensis* characteristics, but these grade with the characters of the typical *F. scruposa* and the validity of the variety *ternatensis* as a distinct morphotaxonomic unit is very doubtful.

Affinities

Although in his original diagnosis Klunzinger (1879) indicated that the primary septa are rather thin, this statement is not repeated in the actual description, which together with the figures, leaves little doubt as to the identify of *F. scruposa*. Klunzinger's type was re-examined by Döderlein (1902) who also gave a thorough description of the species. Due to these good early descriptions and to its characteristic skeletal features, *F. scruposa* has ever since been readily and correctly identified.

Gardiner's type of *F. fieldi*, which was re-examined in the present study, shows some affinities with *F. scruposa*, in particular with the form *ternatensis*.

Distribution

Recorded from the Red Sea and the Halmahera, Ryūkyū and Saipan Islands.

Fungia (Danafungia) horrida Dana, 1846

Synonymy

Fungia horrida Dana, 1846; Edwards & Haime (1860); Quelch (1886); Döderlein (1902); von Marenzeller (1907); Matthai (1924); Boschma (1925); Rossi (1954); Nemenzo (1955a); Stephenson & Wells (1955); Pichon (1964).

Fungia valida Verrill; *sensu* Klunzinger (1879).

Figs. 218-221 *Fungia corona* (× 1.2).

Figs. 218, 219 From Pioneer Bay, Orpheus Island, collecting station 45.
Figs. 220, 221 From Yorke Island, collecting station 13.

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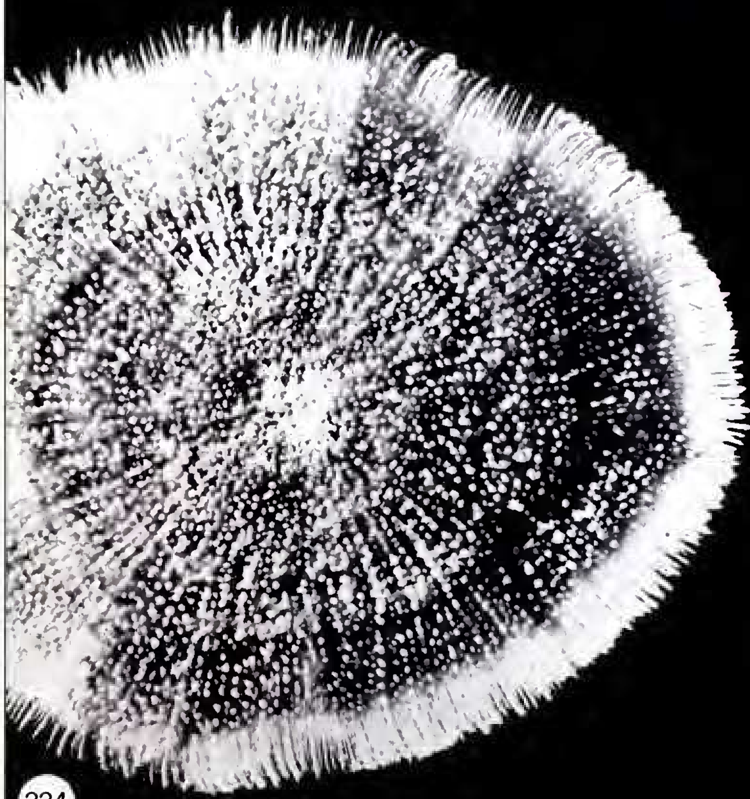

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Material studied

Pearce Cay (3 specimens), **Yorke Island, Murray Island** (5 specimens), **Ashmore Reef, Great Detached Reef** (2 specimens), **Jewell Reef** (3 specimens), **Waining Reef** (2 specimens), **Nymph Island** (2 specimens), **Lizard Island** (14 specimens), **MacGillivray Reef** (3 specimens), **Ribbon Reef** (4 specimens), **Hope Island, Palm Islands** (25 specimens), **Pandora Reef, Gould Reef, Bushy Island-Redbill Reef, Whitsunday Islands** (2 specimens), **Pompey Complex, Swain Reefs** (2 specimens), **Frigate Cay.**

These localities include collecting stations 5, 7, 11, 13, 27, 30, 32, 34, 41, 42, 45, 55, 56, 58, 59, 62, 63, 64, 65, 69, 71, 74, 78, 80, 87, 92, 93, 98, 99, 100, 102, 107, 111, 114, 124, 130, 135.

Previous records from Eastern Australia

Low Isles, Stephenson & Wells (1955).

Characters

Coralla are flat or slightly arched. In a few specimens the upper surface shows a depression between the margin of the corallum and the central furrow; in others, the central part of the upper surface is strongly arched around the mouth fossa. The maximum diameter of the disc is 20 cm.

Principal septa are more exsert than those of higher orders from the periphery to the central fossa, particularly in the inner, arched part of the upper surface. Septal margins bear numerous dentations which are irregular in size and shape. They can be triangular, almost lobate, or narrow and pointed, with either acute or blunt tips (Fig. 231). Dentation tips are often knob-like and inclined away from the dentation axis, either in a septal or tangential direction and the thickening continues down the sides of the dentation as a vertical, irregular ridge, or crest. Dentations of higher orders are smaller and more rounded. The upper part of secondary septa are sometimes perforate. A tentacular lobe is often present on the inward end of their outer part. All septa are covered with small granules or spinules. The columella is well developed and finely spongy.

Costae are markedly unequal. Principal costae reach the central part of the corallum and bear spines. Secondary costae are without spines. They are well developed in the outer part of the under surface, but lose their individuality towards the centre. All costae are laminar near the margins. Towards the centre they become rounded, interrupted (discontinuous) ridges and slightly wavy in outline. Spines of principal costae are tall (up to 7 mm), cylindrical or conical, sometimes bifurcating or branching in all directions. Spine tips are covered with smaller, rounded spinules or granules. Costal spines are mostly smaller and less branching towards the centre of the corallum, where their arrangement in rows is less conspicuous.

The wall is usually imperforate although a few perforations may occur in the marginal part of some coralla.

Affinities

By its costal and septal structure, *F. horrida* comes close to *F. danai.* However, the two species are readily distinguished by the non-perforate nature of the wall of *F. horrida* and in large series, *F. danai* reaches extremes of size, degree of exsertion

Figs. 222-225 *Fungia scruposa* (× 0.8).

Figs. 222, 224 From the Pompey Complex, collecting station 71.
Figs. 223, 225 From Lizard Island, collecting station 11.

of the principal septa and size and shape of the costal spines and septal dentations, which are never attained by *F. horrida*. The latter groups with *F. valida, F. acutidens* and *F. klunzingeri* Döderlein, in the category of *Danafungia* species which do not have a perforate wall. By the regularity of its septal dentations, *F. klunzingeri* stands apart from the other three, which have close affinities with each other. In particular, *F. acutidens* is very similar to *F. horrida* and Döderlein (1902) mentioned the possibility that *F. horrida* may be a derivative of *F. acutidens*. One of the major differences between the two is the thickened principal septa of *F. horrida*.

Distribution

Recorded from the Red Sea, the Indian Ocean (Zanzibar, Madagascar), the Moluccas, the Philippines, the Great Barrier Reef, Fiji and Tahiti.

Fungia (Danafungia) valida Verrill, 1864

Synonymy

Fungia valida Verrill, 1864; Ortmann (1888); Döderlein (1902); Umbgrove (1940).

non Fungia valida Verrill; *sensu* Klunzinger (1879); Quelch (1886) Stephenson & Wells (1955).

Material studied

Murray Island.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are circular, flat, or slightly convex. Septa are equal or subequal. Only those of the highest orders are small; those of the first two or three orders are relatively thick. Septal dentations are triangular, very large, up to 9 mm in length and 8 mm in height. The triangular dentations often have a narrow base and elongate tip, which sometimes becomes styloid, either vertical, or bent inwards or outwards in a radial direction, in a *scruposa*-like manner. Tips of dentations are often spinulose; their margins are sometimes irregularly crenellated. The sides of all septa are covered with numerous small granules and their margins are very irregular. The upper part of higher order septa are perforate. The columella is well developed and finely spongy. Principal costae are low ridges, without the projecting, laminar morphology found in most other species of *Danafungia*. They bear scattered, tall, conical spines, becoming taller and more abundant towards the outer part of the corallum (Fig. 233). Their tips are hirsute, covered with irregular spinules and their sides are granulated. Costae of higher orders are devoid of any ornamentation. They are low, rounded ridges, discontinuous and slightly wavy in outline. The central field of the undersurface bears only a few small scattered spines. The wall is imperforate.

Figs. 226-231 *Fungia horrida*, Figs. 226-230 (× 0.8).

Fig. 226	From Dido Rock, Palm Islands, collecting station 58.
Fig. 227	From Lizard Island, collecting station 99.
Fig. 228	From Great Palm Island, collecting station 92.
Figs. 229, 231	From Fantome Island, Great Palm Island, collecting station 34, Fig. 231 showing septal dentations (× 2.0).
Fig. 230	From Barber Island, Palm Islands, collecting station 93.

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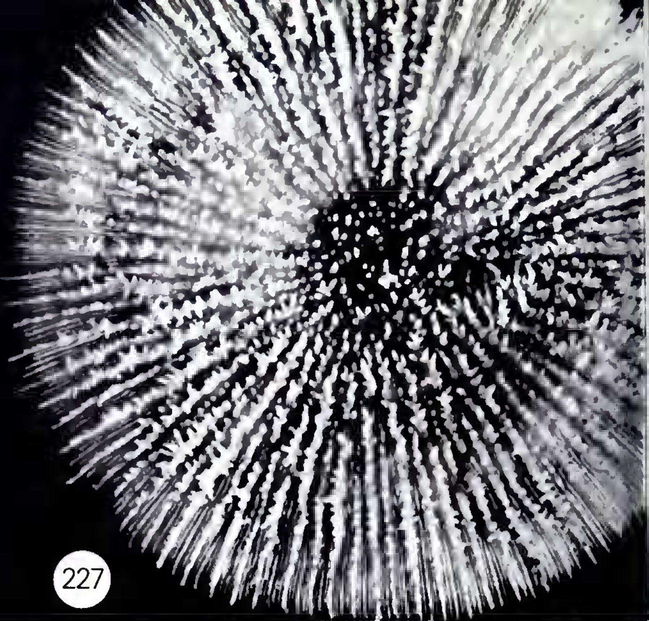

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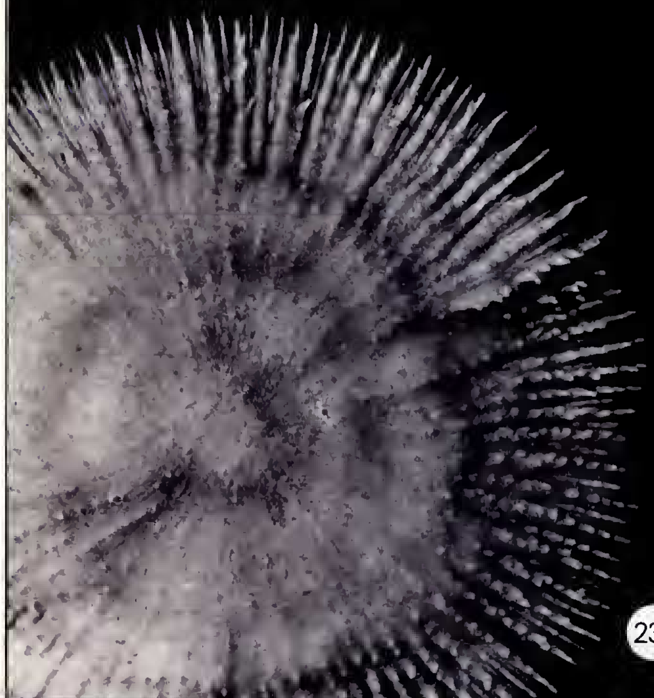

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Affinities

Döderlein (1902) separated *F. valida* from the three other species of imperforate *Danafungia* partly on the basis of its non-laminar costae. This character is certainly not the major distinctive one, since, in large series, several specimens belonging to various other species of *Danafungia* do not have laminar costae, except at the very margin of the corallum.

Fungia valida is clearly distinguished from other species of *Danafungia* by its very large triangular septal dentations and (although Döderlein (1902) made this species an early derivative of the non-perforate *Danafungia*) its affinities could rather be with *F. horrida*, which sometimes has similar large, styloid dentations.

Distribution

Recorded from the western Indian Ocean (Zanzibar), the Moluccas, the Great Barrier Reef, Onotoa and the Canton Islands.

Fungia (Danafungia) klunzingeri Döderlein, 1901

Synonymy

Fungia klunzingeri Döderlein, 1901; Döderlein (1902); van der Horst (1921).

Fungia valida Verrill; *sensu* Stephenson & Wells (1955).

Material studied

Murray Islands (3 specimens), **Lizard Island, Palm Islands** (3 specimens). These localities include collecting stations 26, 30, 34, 58, 91, 99.

Previous records from Eastern Australia

Low Isles, (as *Fungia valida*) Stephenson & Wells (1955).

Characters

Coralla are generally flat but irregularly contorted. In one specimen only, the central part of the upper surface is arched above the central fossa. Septa of the lower cycles are markedly exsert, but only slightly thicker than those of the higher cycles (particularly in their elevated part, near the central fossa). Septal dentations are regular, of comparatively moderate size, triangular or subtriangular, with mostly rounded, knob-like tips. Their vertical axes are thicker than the rest and protrude on both sides as a vertical ridge, irregularly covered with blunt granules, sometimes arranged in discontinuous rows, following the septal margin contour. The ornamentation of higher orders is less prominent, with dentations arranged in irregular lobes. Septa of the highest orders are very perforate. There are no tentacular lobes.

The central fossa is comparatively short, the columella small. Principal costae are well developed, laminar and distinctly project above the undersurface. They are covered with numerous conical spines fused at their base, often slightly compressed laterally and often inclined towards the corallum margin. They bear a few pointed spinules at their tips, and their sides are covered with blunt spinules or rounded granules; 3-5 costae of higher orders, totally devoid of spines, separate the major costae.

Affinities

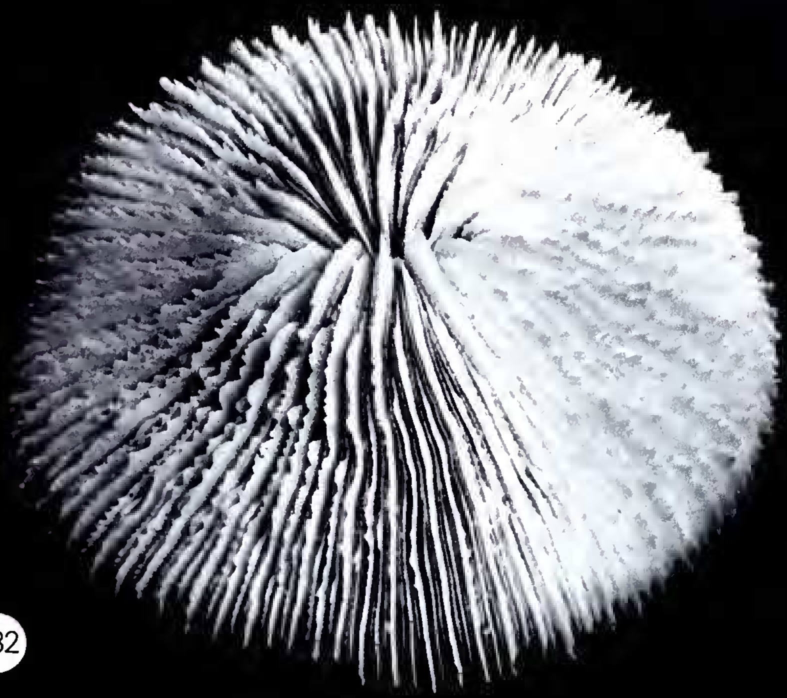
The present series agrees well with Döderlein's (1902) description and figures, except that none (all mature specimens) show any trace of a scar of attachment. This character, however, has a doubtful specific value as Döderlein apparently had only one mature specimen. He mentions the affinity between juvenile *F. klunzingeri* and

F. acutidens although the latter, at least in the adult stages, has very irregular septal dentations. By the very laminar nature of its costae and by the characters of the spines (slightly compressed laterally), *F. klunzingeri* also shows some affinity with *F. corona*, which also has laterally flattened costal spines and (comparatively) even septal dentations. Thus, *F. klunzingeri* bears a similar relationship to *F. corona* as *F. horrida* does to *F. danai*.

Distribution

Recorded from the Red Sea and the Great Barrier Reef.

Figs. 232, 233 *Fungia valida* from Lizard Island, same corallum (× 1.0).



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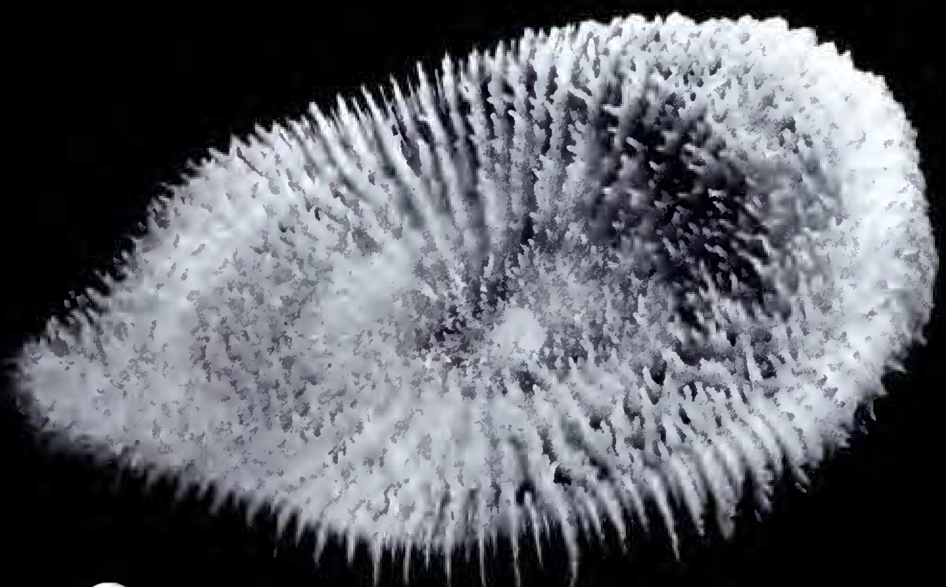

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Subgenus *Verrillofungia* was established by Wells to include the species belonging to the *'repanda'* group of Döderlein.

Coralla are circular, flat, or centrally arched. Costae are unequal cyclically, bearing typically blunt, spinose or granulose spines, which may become branching. Septa bear rounded to triangular dentations, composed of minute fans of trabeculae tending to diverge from the plane of the fan and emerge as irregular ridges, roughly concentric to the edge of the dentation. In septa of higher cycles, the dentations tend to become irregularly spinose.

Four species of *Verrillofungia* are represented in the present collection: *F. repanda* Dana, *F. concinna* Verrill, *F. scabra* Döderlein, and *F. granulosa* Klunzinger.

Fungia fieldi Gardiner has been referred to *Verrillofungia* by Rosen (1971), but Gardiner's species does not belong here. *Fungia samboangensis* Vaughan, the type of which was examined in the U.S. National Musem, pertains to *Verrillofungia; F. adrianae* van der Horst is more doubtful. None of these species has been found in the Great Barrier Reef.

Verrillofungia is well characterised, but shows affinities with both *Pleuractis* and *Cycloseris.* It is probably the oldest member of the genus *Fungia,* derived from *Cycloseris,* and there are clear affinities between some species of *Cycloseris* and *Verrillofungia scabra,* which has comparatively minute septal and costal ornamentations. Affinities with *Pleuractis* are represented by transitional forms between the two subgenera such as *F. adrianae* and, especially, *F. moluccensis.*

Fungia (Verrillofungia) repanda Dana, 1846

Synonymy

Fungia repanda Dana, 1846; Edwards & Haime (1851a, 1860); Verrill (1864); Quelch (1886); Ortmann (1889); Döderlein (1902); Bedot (1907); van der Horst (1921); Boschma (1925, 1929); Faustino (1927); Crossland (1931); Thiel (1932); Yabe & Sugiyama (1935, 1941); Eguchi (1938); Umbgrove (1939, 1940); Nemenzo (1955a); Rossi (1956); Searle (1956); Ma (1959); Pichon (1964); Wells (1966).

Fungia linnaei Edwards & Haime, 1851a; Edwards & Haime (1860).

Fungia fieldi Gardiner, *sensu* Yabe & Sugiyama (1941).

Fungia samboangensis Vaughan; *sensu* Nemenzo (1955a).

Material studied

Pearce Cay (3 specimens), **Yorke Island** (4 specimen), **Murray Islands, Ashmore Reef** (3 specimens), **Sue Islet** (2 specimens), **Tijou Reef, Jewell Reef** (3 specimens), **Lizard Island** (20 specimens), **MacGillivray Reef** (4 specimens), **Plug Reef** (3 specimens), **Low Isles, Palm Islands** (19 specimens), **Gould Reef** (2 specimens), **Bait Reef, Whitsunday Islands** (6 specimens), **Pompey Complex, Swain Reefs** (4 specimens), **Frigate Cay** (7 specimens).

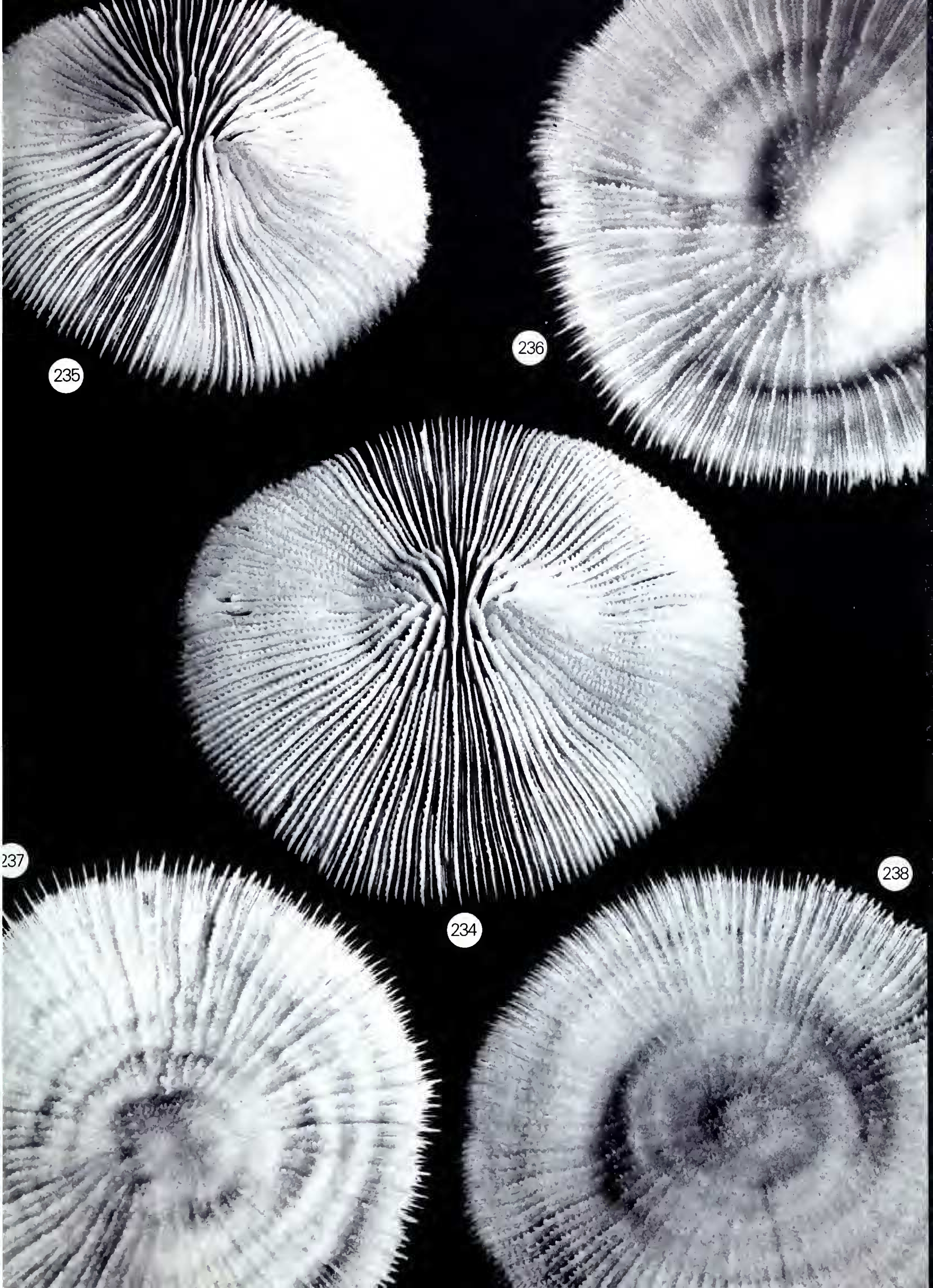
These localities include collecting stations 2, 11, 13, 17, 27, 32, 34, 37, 39, 42, 56, 57, 58, 60, 61, 69, 71, 74, 79, 81, 92, 93, 97, 98, 99, 102, 106, 114, 124.

Previous records from Eastern Australia

Not previously recorded.

Figs. 234-238 *Fungia klunzingeri* (× 0.8).

Fig. 234 From Bowl Reef, collecting station 4.
Figs. 235, 237 From Juno Bay, Fantome Island, Palm Islands, collecting station 43.
Fig. 236 From Maer Island, Murray Islands, collecting station 26.
Fig. 238 From Bullumbooroo Bay, Great Palm Island, collecting station 35.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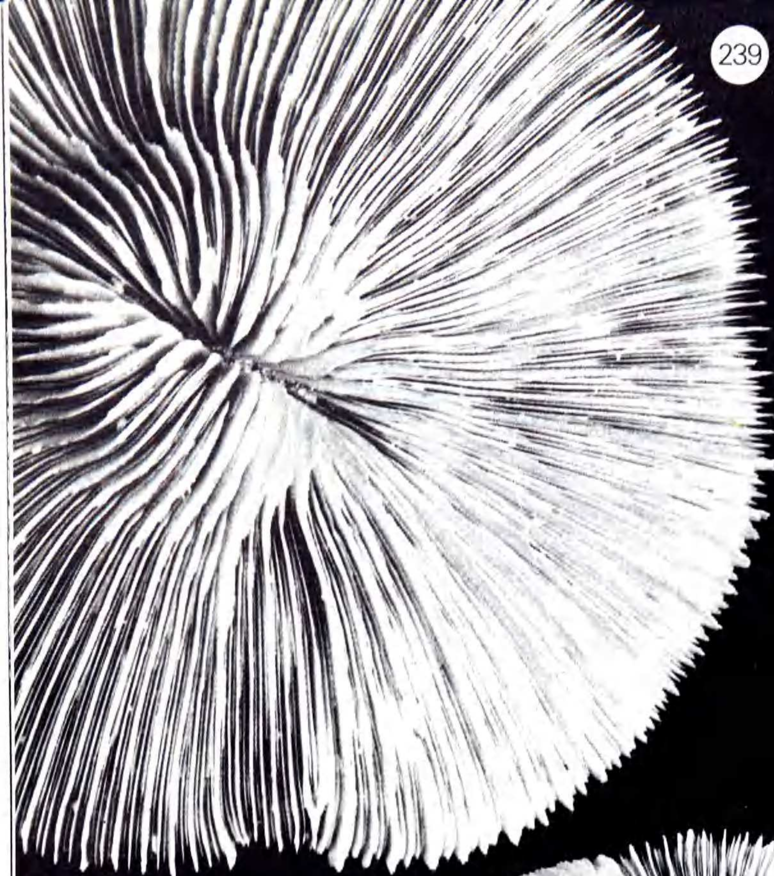

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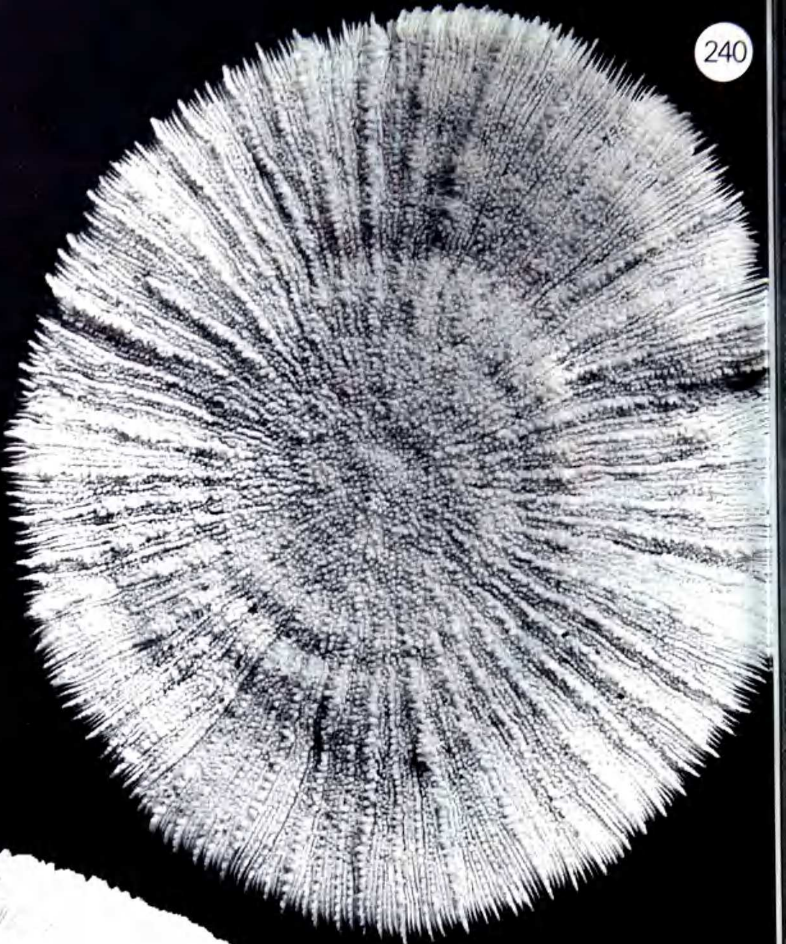

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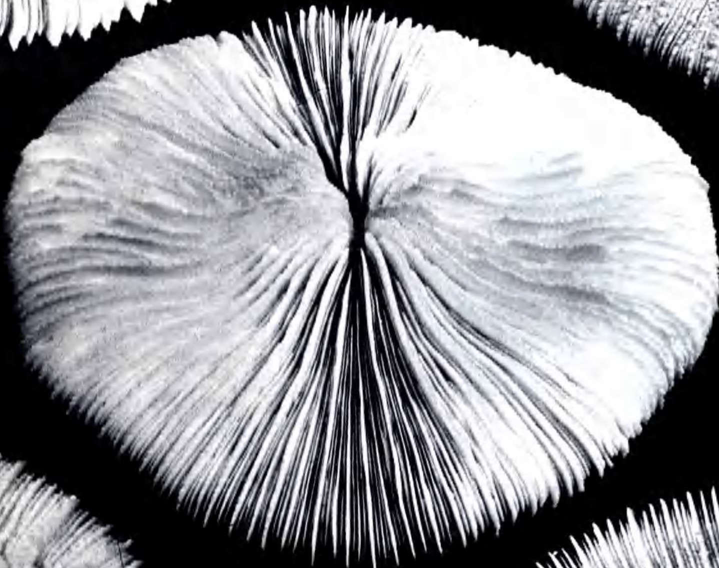

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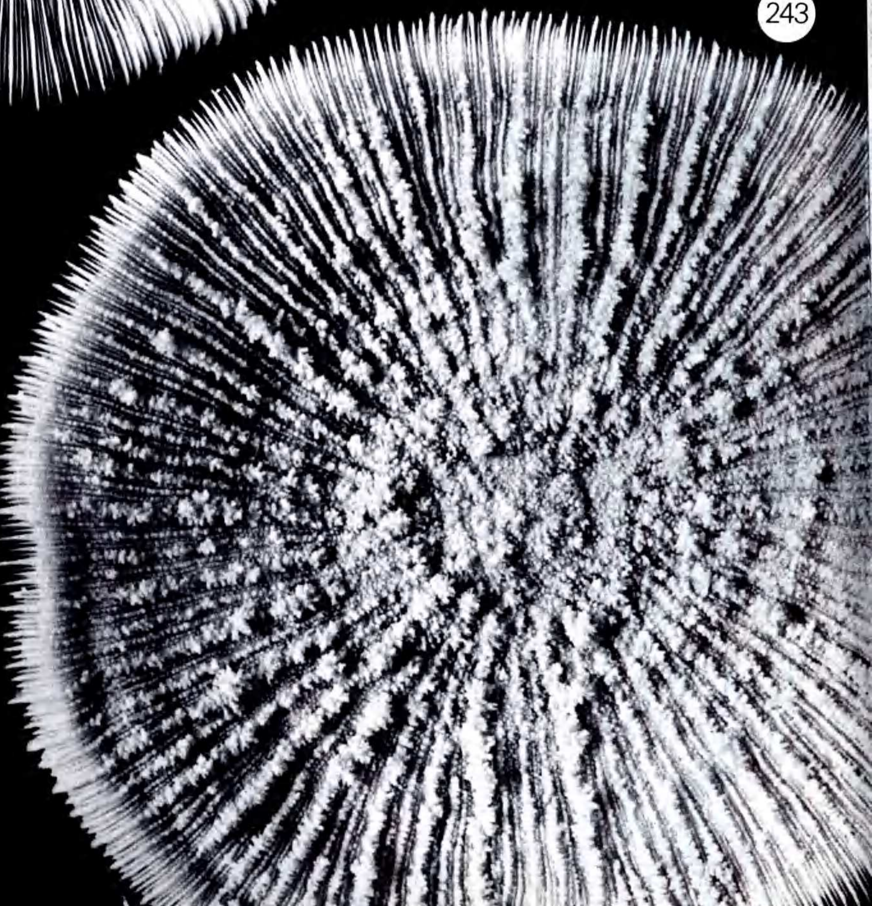


Characters

Coralla are circular or subcircular, up to 30 cm diameter. They are comparatively thick, with a lower surface either flat or concave. The upper surface is flat or strongly arched, with a height up to 6 cm. The central part of the upper surface is hardly arched around the axial fossa and in flat specimens the septal margins are sometimes depressed between the corallum margin and centre. Septal margins of the first two or three orders are more exsert than those of the higher orders near the central fossa (Fig. 244). Septa are equal or subequal at the corallum periphery except for those of the highest order, the margins of which remain 1-3 mm lower. There are no tentacular lobes. Margins of low order septa bear triangular dentations, 1-3 mm high. Two or three more or less continuous ridges, composed of series of granules, run roughly parallel to the septal margins. The lower part of the septal sides bears a few small granules or spines. Dentations of higher orders are smaller and more irregular, obtuse or rounded. Free margins are either laciniate or subentire. The fossa is elongate, comparatively narrow and deep. Septa of higher orders fall vertically in the fossa. The columella is weakly developed.

The lower surface is perforate, the perforations appearing as slit-like fossae, almost extending to the centre of the disc. They are more abundant, however, in the outer half of the corallum. The lower surface bears numerous cyclically unequal costae, the larger and smaller costae corresponding to the lower and higher septal orders respectively. Most costae are low ridges, which appear laminar near the periphery of the corallum, but in a few specimens the laminar character remains conspicuous over at least half the length of the costae. Costae are covered with numerous blunt, granulose spines, club-shaped or branching. In the central area, where no scar of attachment is visible, the spines are usually no longer arranged in radial rows, but are irregularly scattered.

Skeletal variation

Fungia repanda is a comparatively well defined species, with little intraspecific variation. In addition to the above-mentioned variation in corallum shape, there is some variation in the height of septa (from almost equal to alternating, the lower orders being more markedly exsert), the size of dentations, the number of perforations and in the shape of the costal spines, which in some specimens become predominantly hirsute, with numerous, blunt, granulations.

Affinities

The affinities of *F. repanda* with *F. concinna* are discussed with the latter species. The affinities of two other *Verrillofungia* species, *F. fieldi* and *F. samboangensis*, are difficult to assess, for only a few specimens of each have been collected so far. *Fungia samboangensis* is known by its type specimen; Nemenzo (1955a) attributed a further few specimens to it, but did not give any figures and the typical characters of Vaughan's *F. samboangensis* do not emerge from his description. It is probable that Nemenzo's *F. samboangensis* are actually *F. repanda*, hence his comment that '*F. repanda* is so close [to *F. samboangensis*] that identification is quite difficult and uncertain'.

Fungia samboangensis Vaughan differs from *F. repanda* by having fewer, markedly unequal septa, with those of the lower orders being very exsert. The lower part of the costae are conspicuously lamellar, leaving deep, narrow grooves with floors bearing numerous, elongate, slit-like alveoli. Vaughan's type does not fall within the present range of variation of *Fungia repanda* and thus would appear to be a distinct species.

Figs. 239-243 *Fungia repanda* (× 0.7).

Figs. 239, 240, 241, 243 From Great Palm Island, collecting station 92. Figs. 239, 243, same corallum; Figs. 240, 241, same corallum.

Fig. 242 From MacGillivray Reef, collecting station 74.

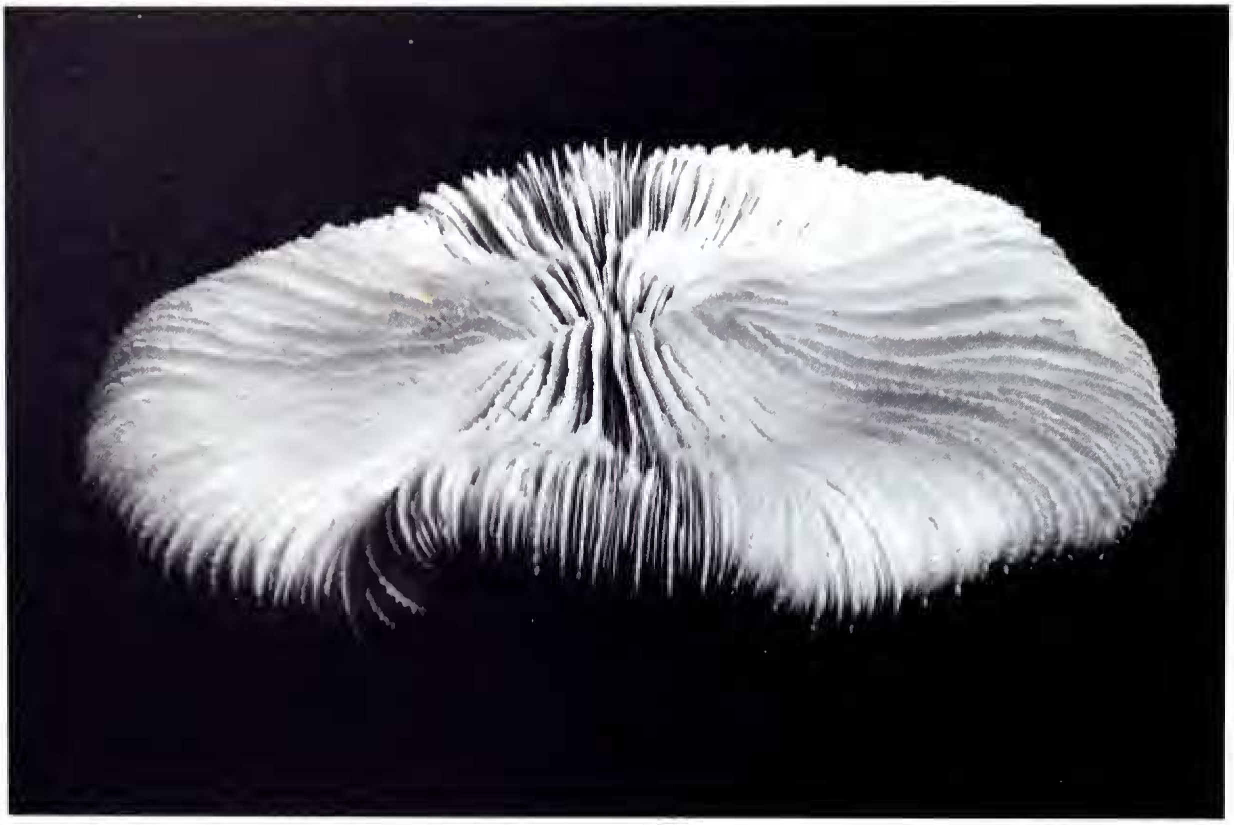


Fig. 244 *Fungia repunda* from Great Palm Island, collecting station 92, showing septal ornamentation (× 0.8).

Fungia fieldi Gardiner is similarly known from only a few specimens. It is very close to, if not identical with, *F. madagascariensis* Vaughan, 1905, the subgeneric affinities of which are with *Danafungia*, not *Verrillofungia*, as stated by Gardiner. *Fungia fieldi* Yabe & Sugiyama, 1941, is a clear synonym of *F. repanda.*

Distribution

Widely distributed in the Indo-Pacific, from the Red Sea and south-west Indian Ocean, to south-east Tuamotu.

Fungia (Verrillofungia) concinna Verrill, 1864

Synonymy

Fungia concinna Verrill, 1864; Quelch (1886); Döderlein (1902); Gardiner (1909); Vaughan (1918); van der Horst (1921); Boschma (1925); Faustino (1927); Hoffmeister (1929); Thiel (1932); Umbgrove (1939, 1940); Yabe & Sugiyama (1941); Wells (1954); Nemenzo (1955a); Stephenson & Wells (1955); Scheer & Pillai (1974).

Fungia patella Verrill, 1864.

Fungia serrulata Verrill, 1864.

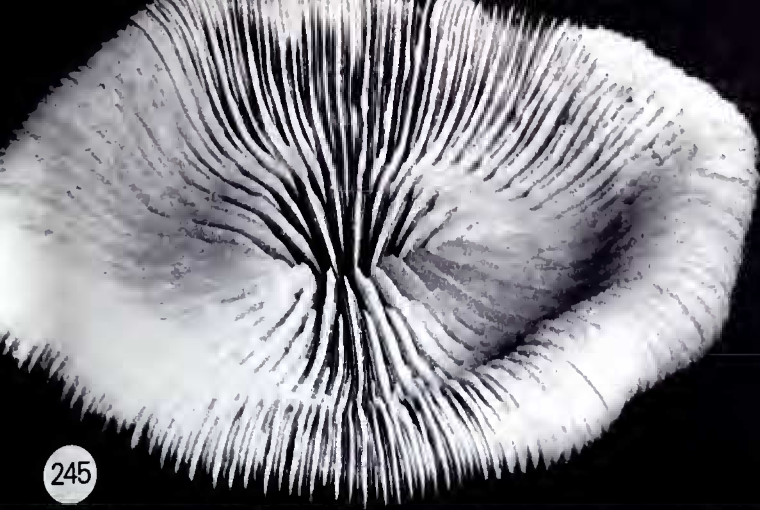
Fungia plana Studer, 1877; Quelch (1886); Gravier (1907, 1911); von Marenzeller (1907); Yabe & Sugiyama (1935).

Fungia agariciformis Dana, 1846.

? *Fungia granulosa* Vaughan, 1906.

Figs. 245-249 *Fungia concinna* (× 0.7).

Fig. 245	From Lizard Island, collecting station 11.
Figs. 246, 248	From Frigate Cay, collecting station 81.
Fig. 247	From Barber Island, Palm Islands, collecting station 93.
Fig. 249	From the Swain Reefs, collecting station 76.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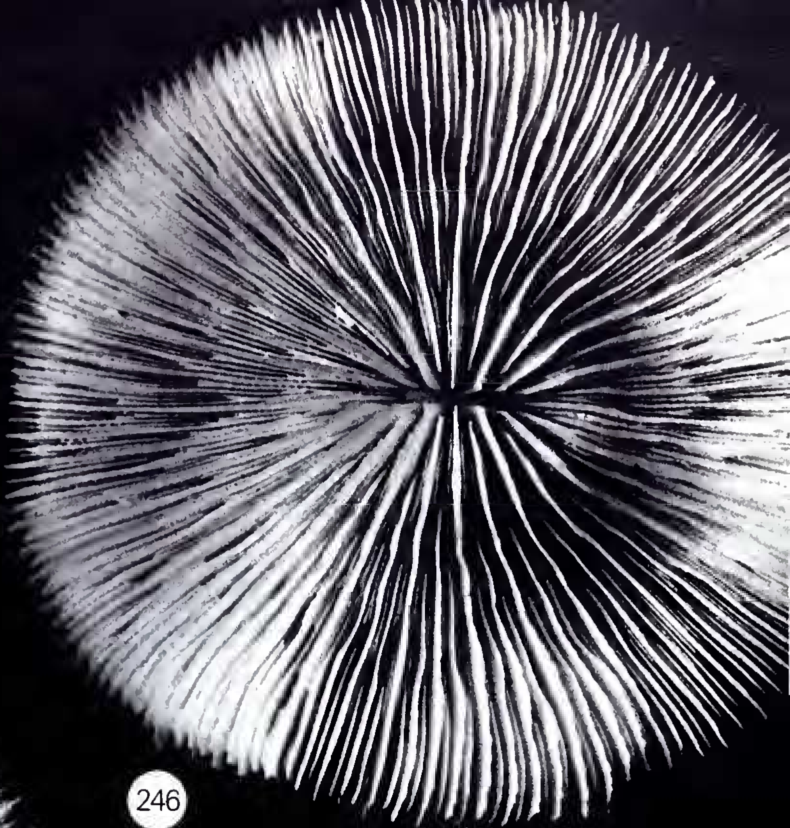
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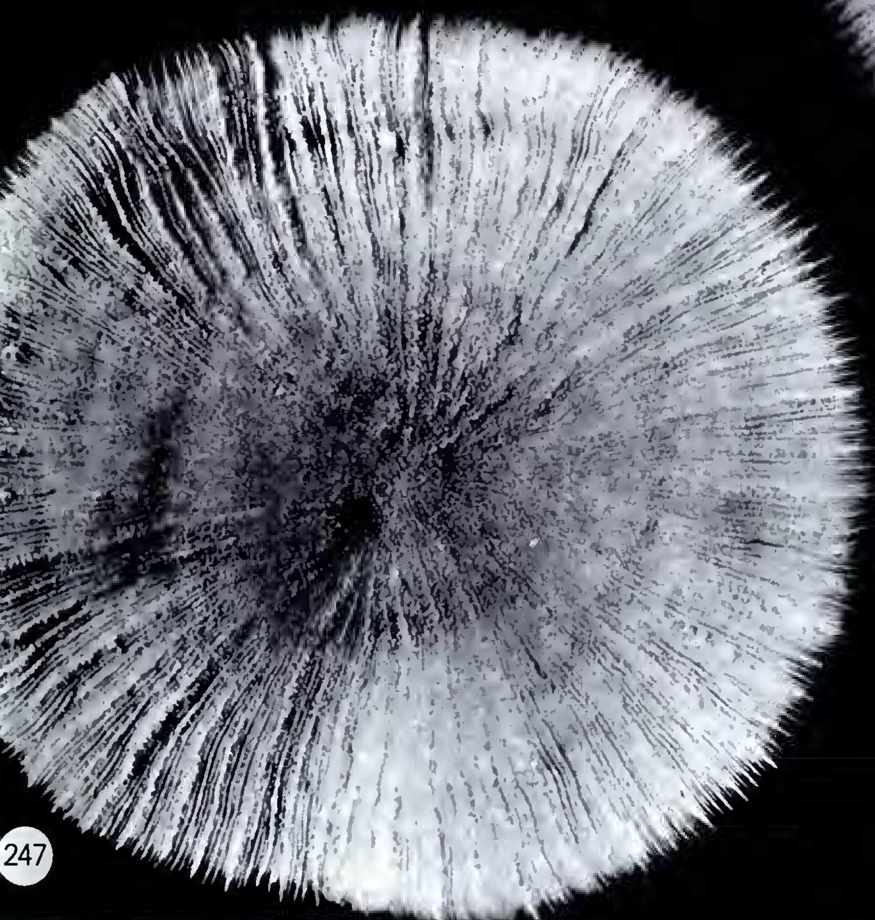
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Material studied

Pearce Cay, Ashmore Reef (3 specimens), **Yorke Island** (3 specimens), **Murray Islands** (2 specimens), **Sue Islands, Great Detached Reef, Tijou Reef** (6 specimens), **Jewell Reef** (6 specimens), **Yonge Reef** (2 specimens), **Lizard Island** (16 specimens), **MacGillivray Reef, Ribbon Reef** (2 specimens), **Plug Reef, Hope Island, Bowl Reef** (2 specimens), **Palm Islands** (16 specimens), **Gould Reef** (2 specimens), **Whitsunday Islands** (2 specimens), **Pompey Complex, Frigate Cay, Swain Reefs** (2 specimens).

These localities include collecting stations 2, 3, 5, 10, 11, 13, 17, 26, 27, 32, 34, 42, 43, 45, 55, 56, 57, 58, 60, 61, 63, 64, 65, 69, 69, 70, 74, 76, 81, 92, 93, 98, 100, 106, 107, 114, 124, 126.

Previous records from Eastern Australia

Murray Islands, Vaughan (1918); **Low Isles,** Stephenson & Wells (1955); **Maori Reef,** Stephenson & Wells (1955); **Fitzroy Island,** Stephenson & Wells (1955).

Characters

Coralla are circular or subcircular, up to 16 cm diameter. Their thickness is very variable. A few specimens have a convex undersurface, with a concave upper surface ('saucer-shaped' coralla with the margins conspicuously higher than the central part, Fig. 245). Only one specimen is strongly arched, with a very concave undersurface. There is little arching around the axial fossa. Septa of the first three orders are more exsert than those of the higher orders near the central fossa. Septa are equal at the periphery, except for those of the one or two highest orders. The upper margins of lower order septa bear triangular or subtriangular dentations which vary continuously in number from 3 to 24 per cm. The margins of the higher orders bear irregular, laciniate spines, or irregular lobes. Sometimes the outer part is subentire. The sides of all septa are regularly covered with small, conical spines. The sides of dentations have the wavy ridges, parallel to the septal margin, which are typical of the subgenus. The axial fossa is elongate, narrow and deep, with a weakly developed columella.

The lower surface is not perforate. Exceptionally, a few shallow alveoli are found near the periphery of the disc. Costae are well developed, numerous, thin, cyclically unequal, and reach almost to the centre of the corallum, towards which their height decreases. They are covered with numerous small spines, generally granular, blunt at the top, sometimes hirsute and branching (Fig. 250). In the central part of the disc, where no scar of attachment is usually visible, spines are no longer in rows, but are irregularly scattered.

Skeletal variation

Fungia concinna displays some variation in the development of septal dentations and costal spines. Septal dentations, particularly in juvenile specimens, can be minute (up to 20-24 dentations per cm). Other, often more heavily calcified specimens have a coarser ornamentation, which almost reaches the size observed in *F. repanda*, about 3 dentations per cm. Costal spines are mostly small sized but can be up to 2-2.5 mm high. The costae also show some degree of variability. In some specimens they are only conspicuous in the outer part of the corallum and are only slightly unequal (in such instances, most of the undersurface appears, to the naked eye, to be covered by spines arranged in rows in the outer part of the corallum, becoming irregularly distributed towards the centre); others have markedly alternating costae clearly visible to the centre of the corallum, with tall blunt spines.

Affinities

Although *F. plana* and *F. concinna* were considered as distinct species by Döderlein, they were synonymised by Gardiner (1909), and this standpoint has been

largely adopted by subsequent authors (Vaughan, 1918; van der Horst, 1921; Boschma, 1925, 1929; Thiel, 1932; Umbgrove, 1940; Yabe & Sugiyama, 1941). The two nominal species were previously separated on the basis of the number of dentations per cm: 3 to 10 for *F. concinna* and 15 to 20 for *F. plana;* however, in a large suite of specimens, these values vary continuously.

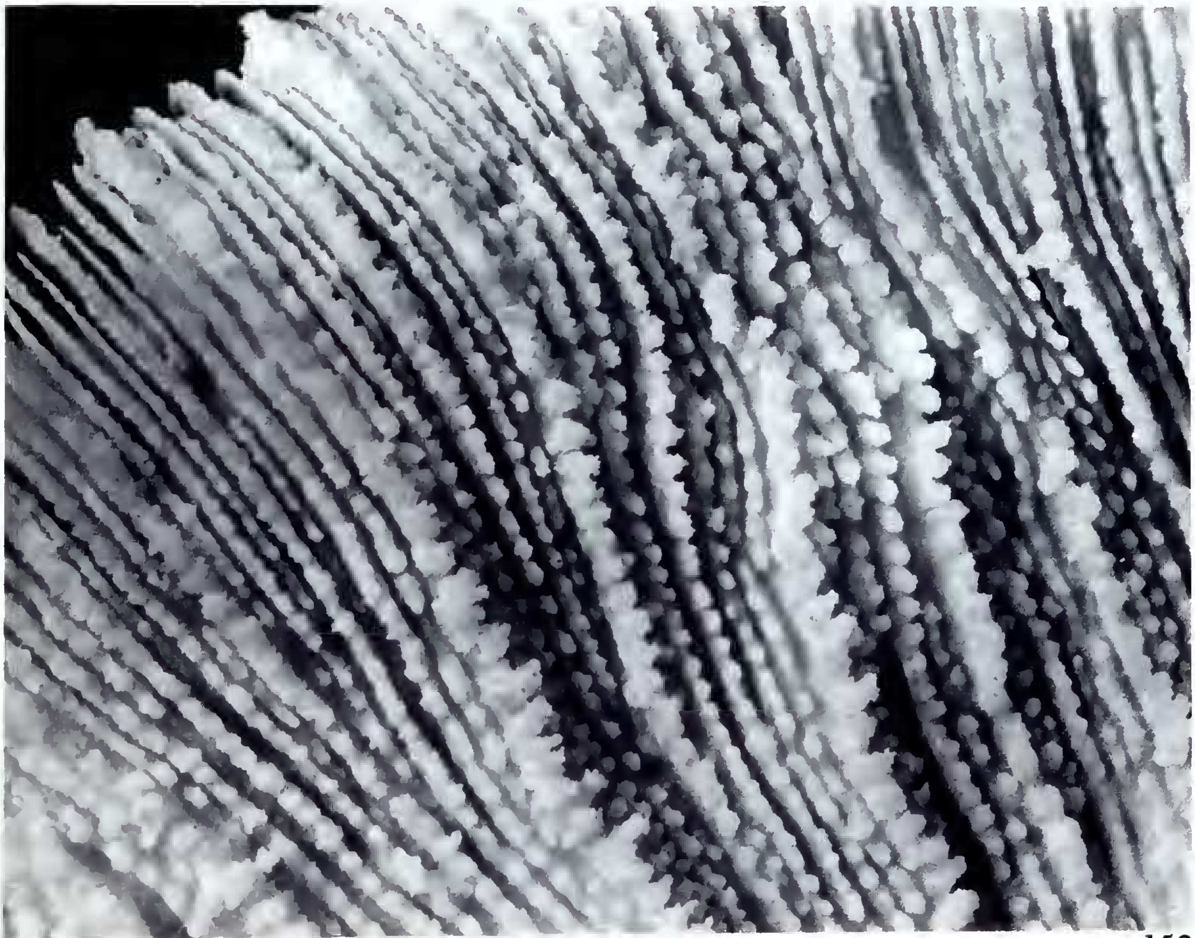
Fungia concinna has close affinities with *F. repanda* and most of the above-mentioned authors (Gardiner excepted) have suggested that they could be part of a continuous series, although none have gone as far as putting them into synonymy. The present studies support Gardiner's conclusion that the two species are distinct. If some specimens can occasionally be referred with doubt to one or other species, they can be readily separated in large series.

The major distinctive character is the perforated wall of *F. repanda,* but this species also has a larger mean size of adult populations and better developed and coarser septal dentations and costal spinulations. Also, septa and costae are generally more numerous in *F. concinna* of similar size.

Distribution

Widely distributed throughout the Indo-Pacific, from the Red Sea and south-west Indian Ocean to Japan and the Tuamotu Archipelago.

Fig. 250 *Fungia concinna* from the Palm Islands, same corallum as Fig. 247, showing details of costal structures (× 5.0).



Fungia (Verrillofungia) scabra Döderlein, 1901

Synonymy

Fungia scabra Döderlein, 1901, Döderlein (1902); van der Horst (1921); Faustino (1927); Nemenzo (1955a).

Material studied

MacGillivray Reef, Palm Islands (3 specimens), **Whitsunday Islands, Pompey Complex, Frigate Cay.**

These localities include collecting stations 41, 55, 60, 71, 74, 81, 97.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are circular or slightly elongate (one specimen of the present series with three centres has a very contorted, irregular outline (Fig. 253)). The disc is flat, or slightly convex, the upper surface is mostly regularly curved, without being arched around the central fossa.

Septa are comparatively thin (thinner than those of *F. granulosa*; see p. 156). They are subequal except for the more convex coralla, where lower orders are more markedly exsert. A small tentacular lobe is present in a few specimens. Septal margins are covered with very small, triangular or conical dentations (up to approximately 40 per cm), which may be replaced by distinct, small, rounded granules. In some coralla, perhaps a result of damage, the margins appear to undulate or become subentire. Septal sides are granular, the granules on the upper part being arranged in rows parallel to the dentation margin and may even fuse into interrupted ridges with wavy outlines. The lower parts of the septa bear scattered small granules or conical spines. The central fossa is oval, the columella is spongiose.

The undersurface bears numerous thin costae, continuous almost to the centre of the corallum, where no scar of attachment is visible. Principal costae are only slightly prominent towards the corallum periphery. On the rest of the undersurface, costae are equal or subequal. They bear numerous small, blunt spines, the surface of which can be slightly spinulose. The wall is not perforate.

Skeletal variation

Fungia scabra remains very poorly known, the only good description being Döderlein's original one. Probably less than 12 specimens have been collected so far. The present series of six specimens shows variation primarily in the shape of the corallum and the thickness and height of the septa. All specimens, however, have a finely dentate septal margin and thin, slightly unequal costae with small blunt spines, which are characteristic of the species.

Affinities

Döderlein (1902) originally expressed the view that *F. scabra, F. plana, F. concinna* and *F. repanda* represent a closely related series of species. Clearly, *F. scabra* has strong affinities with *F. concinna*, the septal dentations and costal spines of the former representing the finer extreme of this series. *Fungia scabra* is also a link between *Verrillofungia* and *Cycloseris*, specimens of the larger species of which are

Figs. 251-256 *Fungia scabra* (× 0.8).

Figs. 251, 254	Same corallum, from between Orpheus and Fantome Islands, Palm Islands, collecting station 60.
Figs. 252, 255	Same corallum from Iris Point, Orpheus Island, Palm Islands, collecting station 55.
Figs. 253, 256	Same corallum from Frigate Cay, Swain Reefs, collecting station 81.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sometimes difficult to differentiate. Thus, for good reasons, Döderlein considered *Verrillofungia* an early off-shoot of the *Cycloseris* group in his phylogenetic tree of the solitary fungiids and *F. scabra* was placed by him at the base of this off-shoot.

Distribution

Recorded from Singapore, Indonesia (Sumatra and Celebes), the Philippines, and the Great Barrier Reef.

Fungia (Verrillofungia) granulosa Klunzinger, 1879

Synonymy

Fungia granulosa Klunzinger, 1879; Döderlein (1902); ? Vaughan (1906b); van der Horst (1921); Boschma (1925); Nemenzo (1955a).

Material studied

Murray Island, Yonge Reef, Lizard Island (4 specimens), **Ribbon Reef, Palm Islands** (6 specimens), **Gould Reef, Whitsunday Islands.**

These localities include collecting stations 3, 28, 34, 37, 55, 56, 63, 93, 97, 113.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are approximately circular, up to 13.5 cm in diameter. The disc is flat or slightly convex, but without reaching the pileiform shape of Klunzinger's specimen. In most cases, the central area of the upper surface is arched above the axial fossa. Septa are numerous, those of lower orders are distinctly wavy (Fig. 258). They are only slightly more exsert than those of higher orders. All septal margins are comparatively thick and are often covered by numerous, well defined, small, triangular denticules, which may be replaced by irregular granules giving a blunt, ragged appearance to the margin. The upper part of the septal sides are also densely covered by irregular granules which tend to be arranged in rows, parallel to the margin. A tentacular lobe is present on septa of higher orders, although it may be only weakly developed. As usual, it occurs where septa of high orders fuse laterally with two septa of the next highest order. In general, the tentacular lobes are wider than the septa and are responsible for the distinctly wavy appearance of the low order septa. The central fossa is narrow and elongate, the columella is spongiose, but poorly developed. The undersurface is densely covered with small papillae or spines which are smooth or delicately spinulose or granulose (Fig. 263). These papillae are arranged in numerous rows corresponding to the costae. Lower order costae are slightly prominent and often bear several series of granulose, blunt, or transversely flattened spines. Small papillae and spines completely cover the undersurface, including the central part of the corallum, where the radial arrangement is no longer visible nor is there any scar of attachment.

The wall is perforate, with small-sized, narrow and elongate perforations abundant.

Figs. 257-262 *Fungia granulosa* (× 1.0).

Figs. 257, 260 Same corallum from Yonge Reef, collecting station 3.
Figs. 258, 261 Same corallum from Elk Cliff, Great Palm Island, collecting station 37.
Figs. 259, 262 Same corallum from Fantome Island, collecting station 34.

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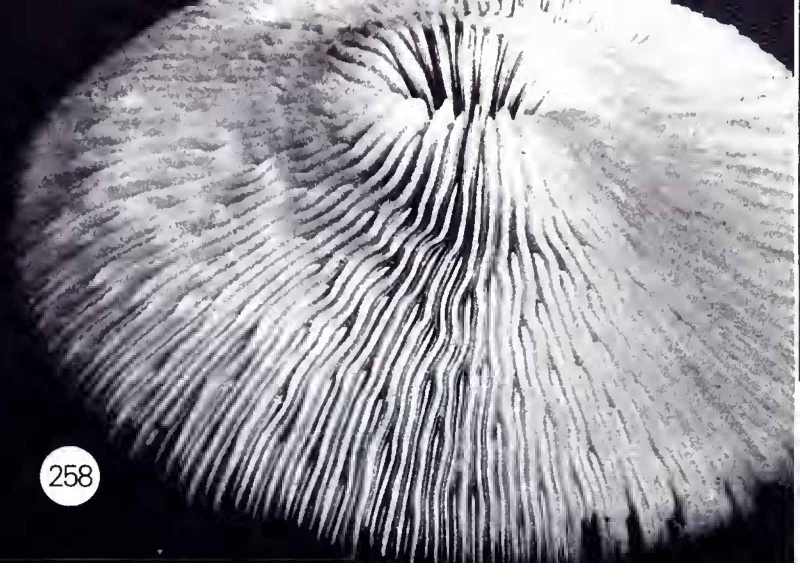

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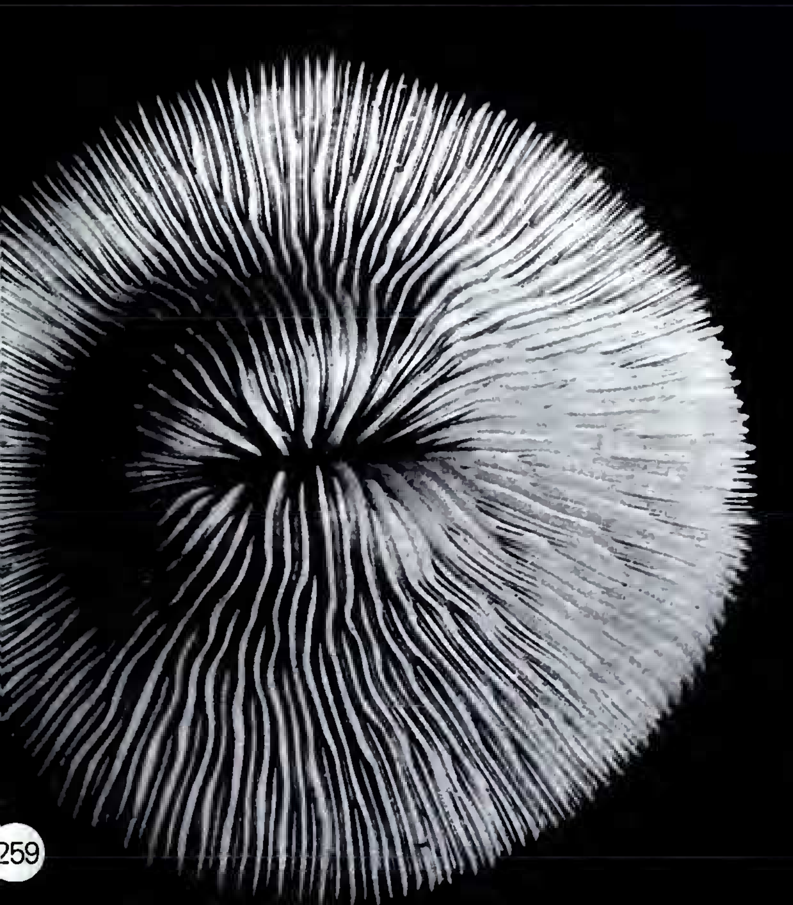

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Skeletal variation

Vaughan (1906b) noted that *F. granulosa* was a rare, poorly known species. Approximately 14 specimens have been recorded, 8 of which are from Banda (Boschma, 1925), but are not well described. Eight out of the 15 specimens of the present series are very similar to each other and are characterised by a flat undersurface, an upper surface arched centrally around the mouth fossa, numerous septa (those of the lower orders wavy in outline) and (for 7 specimens) the presence of tentacular lobes, which may be weakly developed. The major differences with Klunzinger's and Döderlein's descriptions are in the shape of the corallum and in the absence of tentacular lobes. Differences in the shape of the coralla of Döderlein's specimens have already been referred to by Boschma, for his Banda collection. These specimens, however, do not appear to have tentacular lobes. Only one specimen of the present series has the distinctly convex shape described by Klunzinger.

Affinities

Fungia granulosa stands well apart from other *Verrillofungia* species by the obsolete septal dentation, the granular nature of the septal margin and by the high number and small size of the costal papillae or spines. According to Döderlein, *F. scabra, F. plana, F. concinna, F. repanda* form a continuous series, and *F. granulosa* represents a lateral branch deriving from *F. scabra.* The nature of septal dentations and costal spines in these various species supports this hypothesis.

Van der Horst (1919) indicated some similarity between one of his specimens of *F. moluccensis* and *F. granulosa.* As noted below (p. 166) the affinities of *F. moluccensis* could well be with *Verrillofungia,* rather than *Pleuractis* and in that respect *F. moluccensis* could be somewhat distantly related to *F. granulosa.* It should be noted also that the *F. granulosa* of Vaughan (1906b) may be a specimen of *F. concinna.*

Fig. 263 *Fungia granulosa* from Great Palm Island, same corallum as Figs. 258, 261, showing details of costal structures (× 5.0).

Distribution

Recorded from the Red Sea, the Moluccas, the Great Barrier Reef and the Philippines. Also recorded from Japan by Yabe & Sugiyama (1935) but this identification is doubtful.

SUBGENUS *PLEURACTIS* VERRILL, 1864

According to Wells (1966), the subgenus *Pleuractis* (which also includes *Lobactis* Verrill, 1864) is characterised by an elongate corallum, relatively fine, evenly spaced septal dentations, costae nearly reduced to rows of small, lightly spinose or tuberculose spines, and a perforate wall. Although about ten of the then described species of *Fungia* could have been referred to *Pleuractis*, Döderlein (1902) recognised only three, *F. scutaria* Lamarck, *F. paumotensis* Stutchbury and *F. oahensis* Döderlein, the other described species being only varieties or synonyms of these. Since Döderlein, *F. oahensis* has also been generally considered a synonym of *F. scutaria* and Boschma (1929) even suggested that *F. scutaria, F. paumotensis* and *F. oahensis* could all be the one species. Most authors still separate *F. scutaria* and *F. paumontensis*, an opinion supported by the present study.

The status of *F. proechinata* Döderlein remains doubtful. Although placed by Döderlein in the 'echinata' group, which now corresponds with the subgenus *Ctenactis*, it could only be a juvenile of *F. (Pleuractis) paumotensis*, and Döderlein himself mentioned the similarities of costal structure of *F. proechinata* and *F. paumotensis*. Very young specimens of *F. (Ctenactis) echinata* in the present collection also show some similarity in costal structure with *Pleuractis*.

Fungia (Pleuractis) scutaria Lamarck, 1801

Synonymy

Fungia scutaria Lamarck, 1801; Lamarck (1816); Ehrenberg (1832); Edwards & Haime (1860); Klunzinger (1879); Döderlein (1902); Bedot (1907); Vaughan (1907, 1918); Gardiner (1909); van der Horst (1921); Boschma (1925, 1929, 1959); Faustino (1927); Thiel (1932); Umbgrove (1939, 1940); Yabe & Sugiyama (1941); Crossland (1952); Rossi (1954); Wells (1954, 1955b); Nemenzo (1955a); Pichon (1964); Scheer (1972); Scheer & Pillai (1974); Pillai & Scheer (1976).

Fungia dentigera Leuckart 1841; Dana (1846); Edwards & Haime (1851a, 1860); Klunzinger (1879); Ortmann (1892); Gardiner (1905).

Fungia paumotensis Stutchbury; *sensu* Edwards & Haime,1860.

Pleuractis scutaria Verrill, 1864.

Lobactis danae Verrill, 1864.

Lobactis conferta Verrill, 1864.

Fungia placunaria Klunzinger, 1879.

Fungia tenuidens Quelch, 1886.

Fungia verrilliana Quelch, 1886.

Fungia oahensis Döderlein, 1902; Vaughan (1907).

Fungia gravis Nemenzo, 1955a.

Material studied

Bramble Cay, Murray Islands (4 specimens), **Ashmore Reef** (2 specimens), **Great Detached Reef** (4 specimens), **Jewell Reef** (2 specimens), **Yonge Reef** (2 specimens), **Lizard Island** (2 specimens), **Ribbon Reef** (3 specimens), **Palm Islands,**

Old Reef, Bait Reef, Whitsunday Islands, Pompey Complex (3 specimens), **Swain Reefs** (3 specimens), **Frigate Cay, Wistari Reef.**

These localities include collecting stations 1, 3, 5, 7, 9, 11, 27, 29, 32, 61, 63, 70, 71, 75, 77, 81, 98, 103, 106, 107, 109, 128.

Previous records from Eastern Australia

Low Isles, Crossland (1952); **Heron Island,** Salter (1954); **North-West Islet,** Hedley (1927).

Characters and variations

Coralla are oval, irregular, thick and heavy, up to 17 cm long and 11 cm wide. They may have an elongate shape, with approximately straight and parallel sides. They may be either flat or strongly arched (up to 7 cm high). Septa are numerous. In mature specimens these septa are arranged in five 'groups', as described by Gardiner (1905):

(1) About 48 septa, which rise perpendicularly from the axial fossa.

(2) About 48 septa which rise perpendicularly about 2 mm out from the central fossa and have the same height as group 1 septa. Neither of these groups have tentacular lobes.

(3) About 96 very thin septa, commencing 3 mm further out, with upper edges 5-10 mm below those of groups 1 and 2. At a distance of 1 to 4 cm from the axial fossa they rise into the blunt, but generally exsert, tentacular lobe 3-5 mm long projecting up to 3 mm above the general level of the septal margins. After the tentacular lobe they become similar to group 1 and 2 septa in height and thickness.

(4) Up to 192 septa (but this figure is seldom attained) starting similarly with those of group 3 at the level of their tentacular lobes. After 1-3 cm they rise into a tentacular lobe and continue outwards as do the previous groups.

(5) A variable number of septa only recognisable at the ends of the corallum.

The upper free margins of septa beyond their tentacular lobes are ornamented with very small (3 to 4 per mm), regularly triangular serrations. The tentacular lobes are triangular, rounded or square, with blunt, even or slightly crenellated margins. They can be up to 1 mm thick, i.e. much thicker than the septa themselves, hence their wavy appearance, particularly those of groups 1 and 2, as they wind around thick tentacular lobes. The undersurface has a few perforations, at least on the outer half of the corallum. In heavily calcified specimens, perforations are completely lacking. The scar of attachment is inconspicuous and often covered by spines.

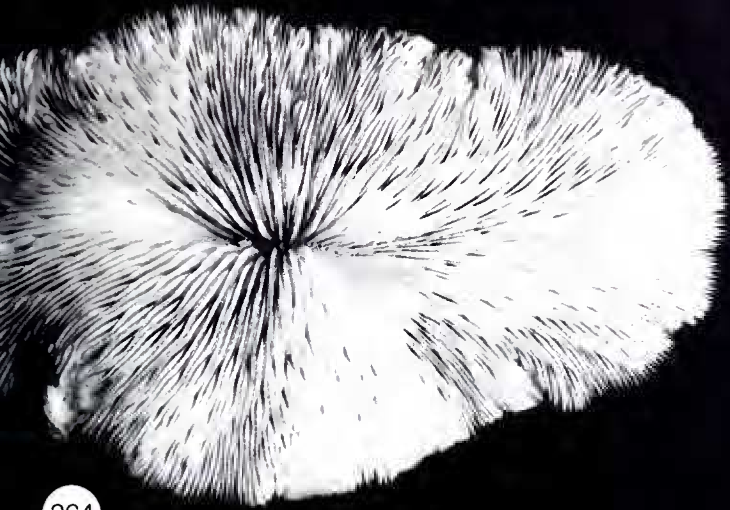
Costae are numerous, clearly distinguishable and prominent over at least half the radius length and often to the centre. They bear numerous spines which vary in shape from blunt, laterally compressed lobes, to conical spines with echinulate tops. The rows of spines become irregular or inconspicuous towards the centre of the corallum.

Affinities

Döderlein (1902) described *F. oahensis* from Hawaii as a new species on the characters of its heavy corallum (flat underneath and very arched above), its numerous humps in the central part of the undersurface, and its skeletal margin, which is divided into numerous lobes by deep, narrow incisions (visible from underneath).

Figs. 264-268 *Fungia scutaria* (× 0.7).

Figs. 264, 265 Same corallum from Great Detached Reef, collecting station 1.
Fig. 266 From Bait Reef.
Figs. 267, 268 Same corallum from the Palm Islands.



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However, Döderlein himself noted the existence of these marginal incisions in *F. scutaria.* The presence of humps or knobs covered with irregularly arranged spines on the central part of the lower surface is a general phenomenon in fungiids with heavily calcified coralla (as already noted by Boschma, 1929). Such humps disturb the regularly radial disposition of the costae, hence the disorganised arrangements of the spines. As noted above, *F. scutaria* shows wide variation in the development of tentacular lobes and in this respect also, *F. oahensis,* in which these lobes are weakly developed but markedly conspicuous, does not differ from *F. scutaria. Fungia oahensis* is therefore considered a synonym of *F. scutaria,* as already suggested by Boschma (1929).

It is also unlikely that *F. gravis* Nemenzo, 1955a is specifically different from *F. scutaria,* but Nemenzo's description and figures are not adequate for a definite conclusion.

Distribution

Widely distributed in the western Indian Ocean (Red Sea to South Africa) and the Pacific, from Japan and the Great Barrier Reef, eastward to Hawaii and the Tuamotu Archipelago.

Fungia (Pleuractis) paumotensis Stutchbury, 1833

Synonymy

Fungia paumotensis Stutchbury, 1833; Dana (1846); Quelch (1886); Döderlein (1902); Bedot (1907); Vaughan (1907); van der Horst (1921); Matthai (1924); Boschma (1925, 1929); Hoffmeister (1925); Faustino (1927); Eguchi (1938); Umbgrove (1940); Yabe & Sugiyama (1941); Crossland (1952); Nemenzo (1955a); Stephenson & Wells (1955); Ma (1959); Scheer & Pillai (1974).

Fungia scutaria Lamarck; *sensu* Dana (1846); Duncan (1884); Quelch (1886).

Pleuractis scutaria Lamarck; *sensu* Verrill, 1864.

Fungia carcharias Studer, 1877.

Fungia plana Studer, 1877.

Material studied

Big Mary Reef, Yorke Island (7 specimens), **Pearce Cay** (3 specimens), **Darnley Island, Murray Island** (6 specimens), **Aureed Island, Ashmore Reef** (4 specimens), **Sue Island, Great Detached Reef, Tijou Reef** (2 specimens), **Bewick Island** (3 specimens), **Jewell Reef** (6 specimens), **Lizard Island** (7 specimens), **MacGillivray Reef** (4 specimens), **Ribbon Reef** (4 specimens), **Plug Reef** (2 specimens), **Hope Island, Bowl Reef, Palm Islands** (32 specimens), **Whitsunday Island** (4 specimens), **Pompey Complex** (3 specimens), **Frigate Cay, Swain Reef** (2 specimens).

These localities include collecting stations 2, 5, 7, 10, 11, 13, 17, 18, 27, 32, 34, 41, 42, 43, 55, 56, 57, 58, 60, 61, 63, 64, 66, 69, 70, 71, 74, 81, 89, 90, 92, 93, 97, 98, 99, 103, 106, 107, 124, 125, 131, 133, 139.

Previous records from Eastern Australia

Low Isles and vicinity, Crossland (1952); **Low Isles,** Stephenson & Wells (1955).

Figs. 269-272 *Fungia paumotensis* (× 0.7).

Fig. 269 From Great Palm Island, collecting station 92.
Fig. 270 From Jewell Reef, collecting station 61.
Fig. 271 From MacGillivray Reef, collecting station 74.
Fig. 272 From Fantome Island, Palm Islands, collecting station 34.


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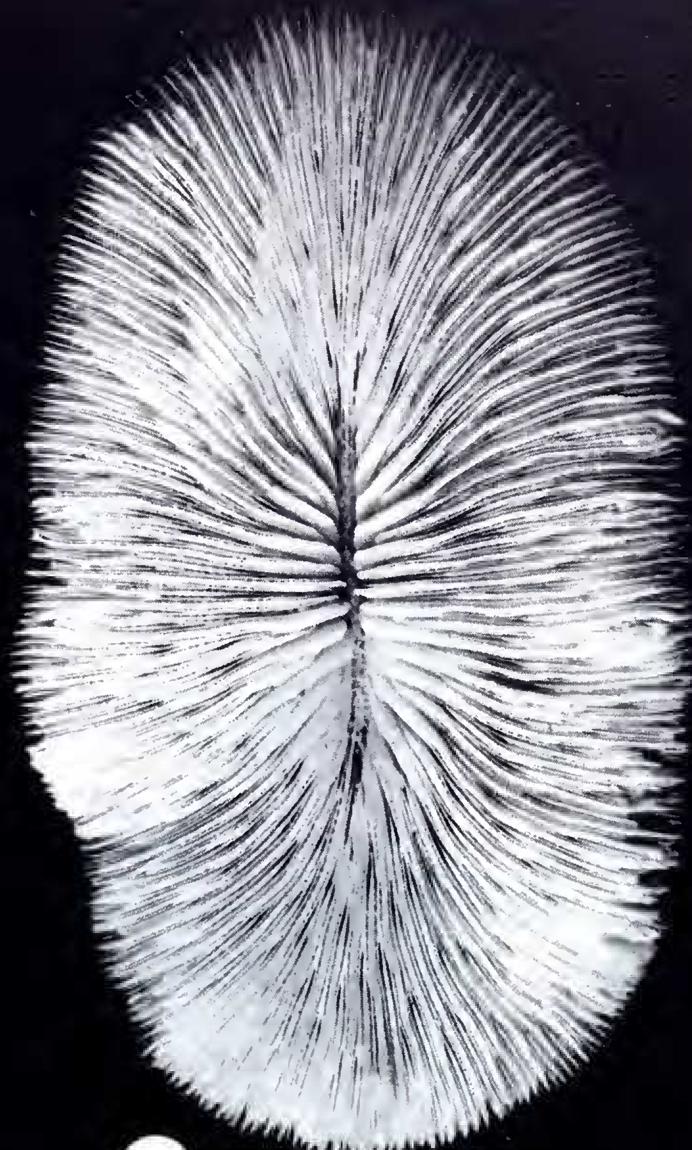
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Characters

Coralla are elongate, with approximately straight, parallel sides; rarely they are irregularly oval. Maximum dimensions are length 25 cm, width 13.5 cm, height 8 cm. Coralla are thick and heavy, either flat or strongly arched. As with some *F. moluccensis* and *F. scutaria*, the central part of the upper face is sometimes strongly arched around the axial fossa (Fig. 269), even in coralla with a flat lower surface. In such instances, the upper and central part of lower order septa are slightly thickened. Septa are straight from the mouth fossa to the corallum margin, or only slightly wavy. The upper margins of higher order septa are, in their inner part, several mm below that of the lower order septa. After fusion with 2 septa of the next highest order (one on each side) the upper margins rise and may become almost level with the upper margins of the principal septa. There is, however, much variation in the size of the septa. In most specimens, septa become equal or subequal near the periphery of the corallum; in some they remain strongly alternating. Their upper margins are usually ornamented with small triangular or subtriangular irregular dentations, but these may be absent. Tentacular lobes are absent. Up to 6 supernumerary, secondary centres have been observed in a few specimens. The undersurface has well developed, equal or subequal costae towards the periphery; these sometimes become swollen and elevated towards the disc centre. These costae are mostly laminar, becoming crenellated near the periphery and discontinuous towards the centre, where they are gradually replaced by rows of laterally compressed lobes, then by cylindrical, blunt spines, which become irregular. No scar of attachment is apparent, except in juvenile coralla (<8 cm long). Perforations are visible on the outer part of the undersurface.

Affinities

The difficulty in distinguishing (particularly juvenile) *F. scutaria* from *F. paumotensis* has led several authors from Quelch (1886) to Crossland (1952) (including Boschma, 1929 and Umbgrove, 1940) to consider these forms synonymous. However, Boschma's suggestions were merely tentative and certainly Rossi (1956) went well beyond his intentions when she wrote '*Fungia paumotensis* Stutch. is specifically identical to *Fungia scutaria* Lamarck with which one observes all possible gradations (Boschma, 1929)'. It appears that Boschma's and Umbgrove's understanding of the two species was largely obscured by the fact that *F. oahensis* was then doubtfully considered a distinct species. Nevertheless, they cite the two species separately, thereby adhering to the accepted situation.

In most cases the two species can be distinguished on the basis of gross morphology: an oval shape, equal septa with thin margins, and an undersurface lobed at the periphery in *F. scutaria;* an elongate shape, with subequal or alternating septa with thick margins in *paumotensis.* They can also be distinguished by their septal structure and disposition: the presence of tentacular lobes in *F. scutaria* and the lateral fusion of septa of the higher orders in *F. paumotensis.*

Fungia moluccensis is probably closer to *F. paumotensis* than to *F. scutaria* and Boschma (1925) stated: 'In this species [*F. paumotensis*] there are some aberrant forms which present peculiarities as are found normally in *Fungia moluccensis'.* Similarities between these two species are mostly in the central swelling of the oral side, which is well developed and almost constant in *F. moluccensis,* but less common in *F. paumotensis.* Thus, the present series has a continuous gradation between completely flat specimens and those showing a well developed, almost *moluccensis*-like central elevation around the mouth fossa (Fig. 269). Other similarities include the thickening of the upper and inner parts of the lower order septal margins (which are slight in some *F. paumotensis,* but well developed and constant in *F. moluccensis*) and the infrequent existence of supernumerary centres. The two species differ markedly in the nature of the costal structures; in *F. moluccensis,* costae are

distinctly alternating in size and are covered with irregular blunt spines or granules, arranged in transverse rows at the corallum periphery. By this character, *F. moluccensis* departs not only from *F. paumotensis*, but from the subgenus *Pleuractis* as a whole, which suggests affinity with *Verrillofungia*.

Distribution

Widely distributed from the Red Sea and Madagascar to the Andaman and Nicobar Islands in the Indian Ocean and east from the Celebes and Japan to the Tuamotu Archipelago in the Pacific. Also recorded by Quelch from Hawaii.

Fungia (Pleuractis) moluccensis van der Horst, 1919

Synonymy

Fungia moluccensis van der Horst, 1919; van der Horst (1921); Boschma (1925, 1929).

Fungia somervillei Gardiner; *sensu* Matthai (1924, *pars*); Scheer & Pillai (1974).

Material studied

Bramble Cay, Big Mary Reef (2 specimens), **Yorke Island, Murray Islands** (2 specimens), **Bewick Island, Jewell Reef, Lizard Island** (3 specimens), **Low Isles, Palm Islands** (38 specimens), **Pandora Reef, Whitsunday Islands** (4 specimens), **Frigate Cay**.

These localities include collecting stations 12, 24, 28, 29, 32, 34, 38, 41, 45, 55, 57, 58, 59, 81, 90, 91, 93, 96, 97, 98, 111, 126, 128, 131.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are extremely irregular in shape (Fig. 756), usually irregularly elongate or oval and comparatively thin at the periphery and strongly arched on the oral surface, around the central mouth fossa. They may remain attached to the substratum until the individual has reached adult size, and can even remain adherent in the adult stage along most of the undersurface. The latter is therefore dead and usually covered with encrusting invertebrates. Two major morphological types with numerous intergrades are derived from this peculiar situation:

(1) Coralla that are attached only centrally, are generally flattened and thin, and have a large scar of attachment (Fig. 279), or are still attached to the substratum, but with most of the undersurface free.

(2) Coralla which are very contorted and adherent to the substrate along most of the undersurface, the latter being a rusty colour and having hardly visible or no costal structures except towards the corallum margins (Fig. 282). Even in very flat or contorted coralla, the central swelling around the oral fossa remains conspicuous, or at least visible.

Septa are unequal. Those of the first two orders are equal in height at the corallum margin, but first order septa are more exsert around the mouth fossa where both orders become thickened and spongiose in structure. They are sometimes very sinuose, with a zig-zag pattern along most of their length. Septal margins are irregular; they sometimes have small triangular dentations followed downwards by a vertical series of granules. More commonly, the septal margins are granular, with a rough, ragged appearance. Irregular perforations occur between the vertical series of granules when these are conspicuous.

Up to 12 supernumerary centres, some poorly defined, may be present. Some are

associated with surface irregularities (frequently associated with boring bivalves and polychaetes), on and around which the septa are extremely contorted (with elements at right angles to the normal radial direction); some are developed in the central furrow. Costae are numerous, mostly equal or subequal. Coralla with encrusted undersurfaces may have costal structures observable only near the periphery. In some coralla, the costae are unequal, especially near the periphery. Principal costae bear spines in several irregular rows which are distinctly compressed in a direction perpendicular to that of the costa. Secondary costae are thin, laminar, occasionally slightly wavy in outline. Their margins are lobate, or bear numerous granules or blunt spines which are often radially compressed.

Affinities

The present series of *F. moluccensis* is highly polymorphic. Some specimens resemble van der Horst's syntypes in being thick, regularly oval, with the central part of the upper surface strongly arched above the mouth fossa (Fig. 273). Some superficially resemble *Cycloseris somervillei* in being thin and flat, with a well defined but small and narrow arch above the mouth fossa. Others are very irregular and contorted, with numerous secondary mouths and a partly or entirely dead undersurface.

Because of this polymorphism, this species has frequently been misidentified. Under *F. somervillei*, Matthai probably referred to a mixture of both *F. somervillei* (= *Cycloseris somervillei*) and *F. moluccensis*, as some of the characters in his description (e.g. perforate septa) are typical of *F. moluccensis* and his Plate IX, Fig. 3 is clearly *F. moluccensis*. Similarly, Scheer & Pillai have identified as *F. somervillei* a specimen of *F. moluccensis* from the Nicobar Islands.

The nearest ally to *F. moluccensis* is probably *F. paumotensis*, an opinion already expressed by Boschma (1925). The arched central part of the upper surface and the thickening of the inner portion of the principal septa may be similar in both species. *Fungia paumotensis*, however, has thicker, heavier coralla, and markedly different costae which are crenellated or form rows of laterally compressed lobes. Boschma (1925) also noted affinities with *Cycloseris cyclolites*.

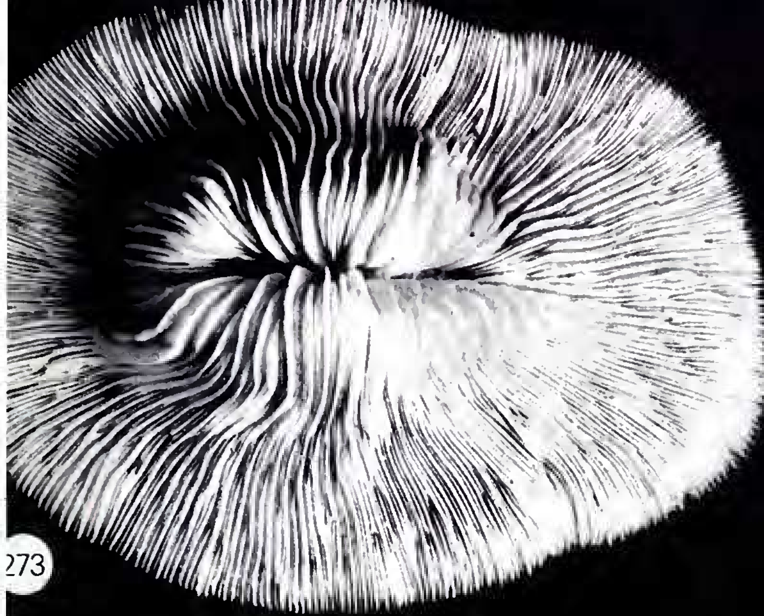
Fungia moluccensis is placed in the subgenus *Pleuractis* primarily on the basis of corallum shape and septal structures. Costal structures, however, are not typical of that subgenus. The radially compressed nature of the costal lobes or granules is not very pronounced, and in some specimens the outer part of the costae are markedly unequal in size. In that respect, *Fungia moluccensis* shows convergence with *Verrillofungia* although this may not necessarily imply direct phylogenetic relationship.

Distribution

Recorded from the Red Sea, the eastern Indian Ocean, the Nicobar and Mergui Islands, the Moluccas, the Philippines and the Great Barrier Reef.

Figs. 273-278 *Fungia moluccensis* (× 0.8).

Fig. 273 From Fantome Island, Palm Islands.
Fig. 274 From Curacao Island, Palm Islands, collecting station 56.
Fig. 275 From Dido Rock, Palm Islands, collecting station 58.
Fig. 276 From Orpheus Island, Palm Islands, collecting station 91.
Fig. 277 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 96.
Fig. 278 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.



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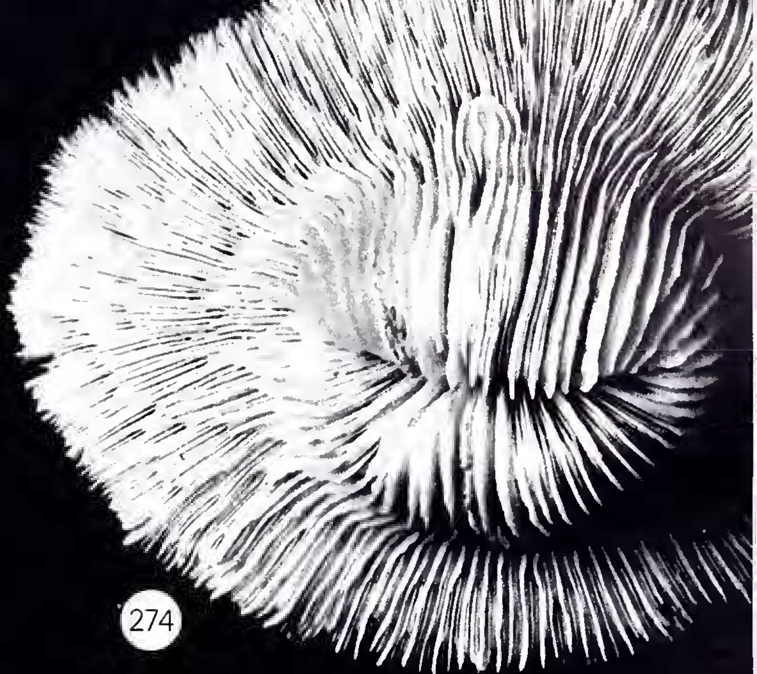

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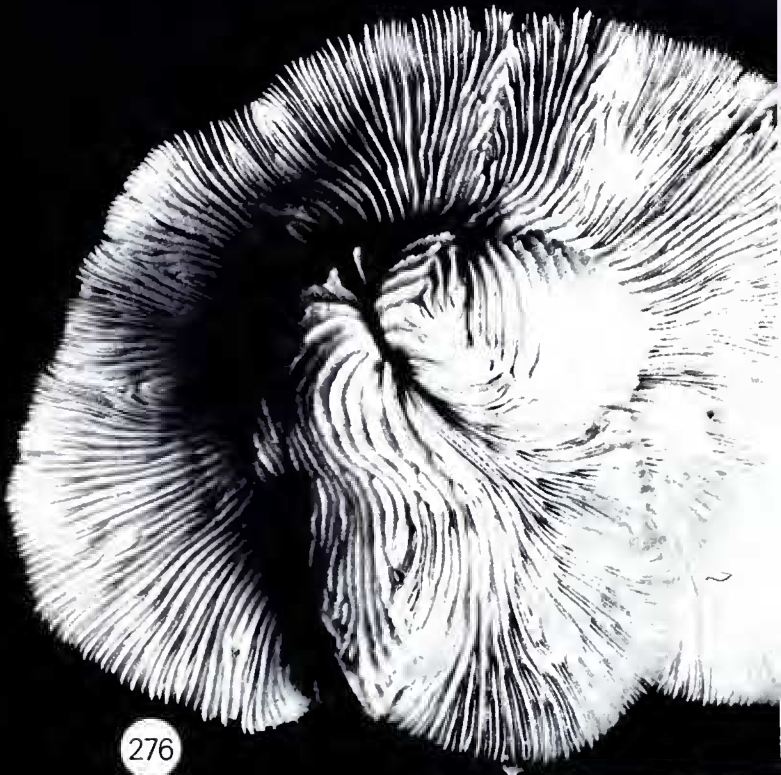

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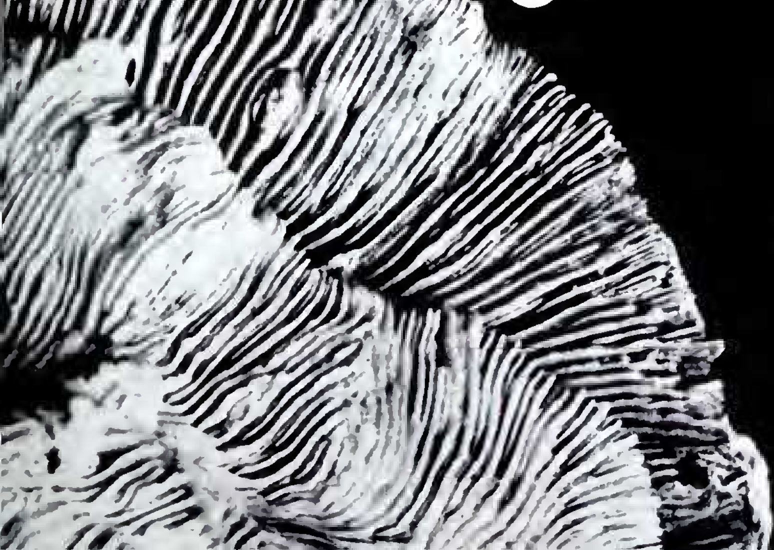

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Subgenus *Ctenactis* Verrill, 1864

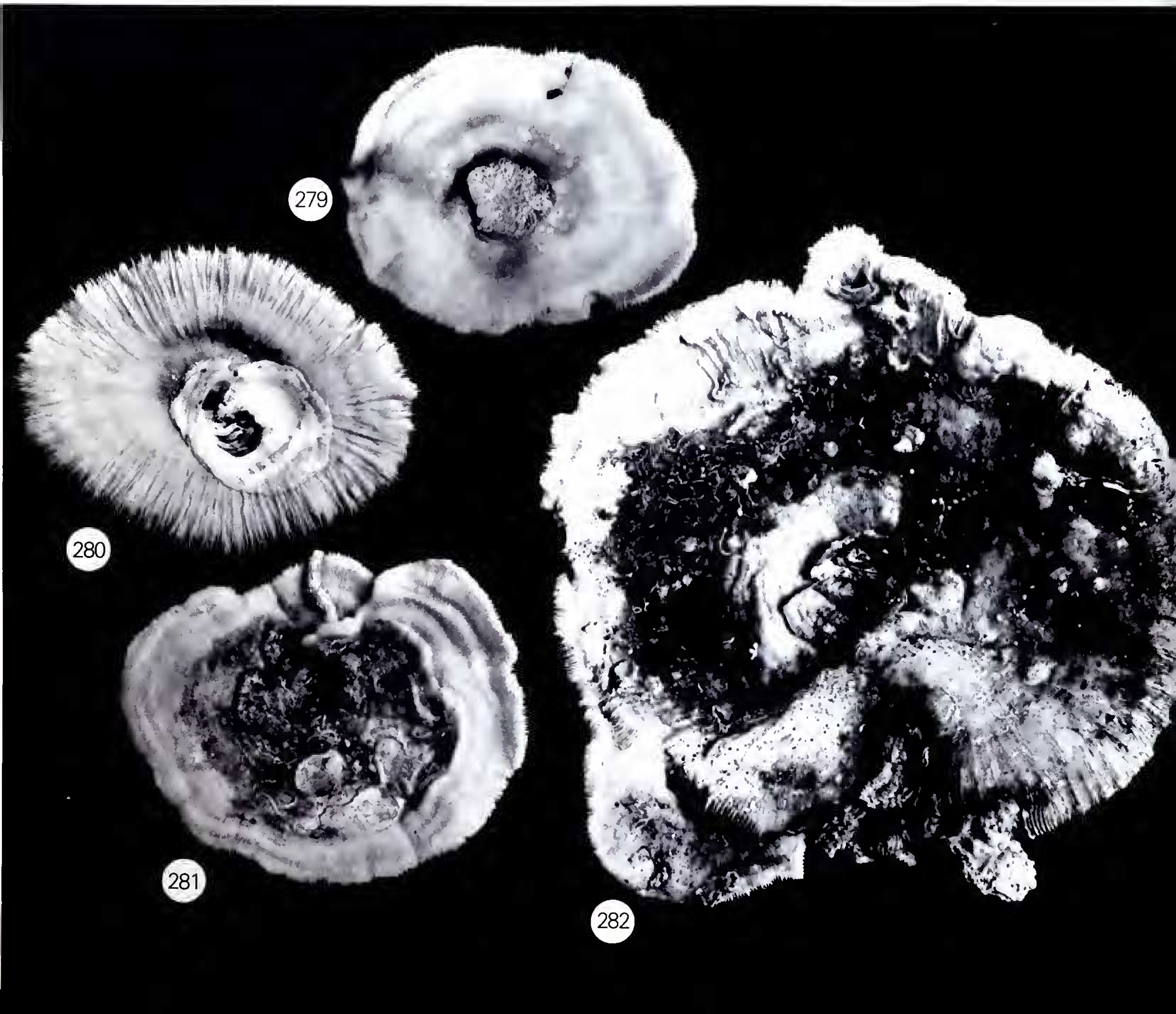
Ctenactis is characterised by an elongate corallum (more so than in *Pleuractis*), with coarse, elongated septal dentations at least 1.5 mm apart and composed of numerous, strongly diverging, trabeculae. Costae are unequal, with strong, arborescent spines.

The subgenus includes only one, or possibly two species (*F. echinata* (Pallas) and *F. proechinata* Döderlein) (see p.171).

Many authors have also included *F. simplex* (= *Herpolitha simplex* Gardiner) in Ctenactis, due to similarities in septal and costal structures. The latter, however, belongs to the genus *Herpetoglossa*, despite its inclusion in *Fungia* by Gardiner (1909) and Matthai (1924).

Figs. 279-282 *Fungia moluccensis* (× 0.5).

Fig. 279 From Dewar Island, Murray Islands, collecting station 28.
Fig. 280 From Curacao Island, same corallum as Fig. 274.
Fig. 281 From Orpheus Island, same corallum as Fig. 276.
Fig. 282 From Nara Inlet, Hook Island, same corallum as Fig. 277.



Fungia (Ctenactis) echinata (Pallas, 1766)

Synonymy

Madrepora echinata, Pallas, 1766.

Fungia pectinata Ehrenberg, 1834; Leuckart (1841); Dana (1846).

Haliglossa echinata (Pallas); Ehrenberg, 1834; Klunzinger (1879).

Herpetolithus ehrenbergi Leuckart, 1841.

Herpetolithus ruppellii Leuckart, 1841.

Fungia ehrenbergi (Leuckart); Dana (1846); Edwards & Haime (1851a, 1860); Studer (1877); Ortmann (1888).

Fungia gigantea Dana 1846.

Fungia asperata Dana, 1846.

Ctenactis echinata (Pallas); Verrill, 1864.

Haliglossa pectinata Klunzinger, 1879.

? *Fungia proechinata* Döderlein, 1902.

Fungia brachystoma Thiel, 1932.

Fungia echinata (Pallas); Edwards & Haime (1851a, 1860); Studer (1877, 1901); Döderlein (1902); Vaughan (1907); Gravier (1907, 1911); Gardiner (1909); (*pars*); Matthai (1924); Boschma (1925); Faustino (1927); (*pars*) Thiel (1932a); Ma (1937); Umbgrove (1939, 1940); (*pars*) Yabe & Sugiyama (1941); Crossland (1952); Wells (1954); Rossi (1954); Nemenzo (1955a); Searle (1956); Ma (1959); Scheer (1967); Scheer & Pillai (1974).

This synonymy of *F. echinata* may be incomplete because of the confusion between *F. echinata* and *Herpetoglossa simplex* (Gardiner, 1909). It has not been possible to examine all specimens of former authors and even after Gardiner's paper, the two species have sometimes not been separated, e.g. by Matthai (1924), Thiel (1932) and Yabe & Sugiyama (1941).

Material studied

Bramble Cay, Darnley Island, Yorke Island (2 specimens), **Murray Islands** (3 specimens), **Ashmore Reef, Sue Islet, Great Detached Reef** (2 specimens), **Jewell Reef** (5 specimens), **Lizard Island** (20 specimens), **Ribbon Reef, Plug Reef, Palm Islands** (14 specimens), **Whitsunday Islands, Swain Reefs** (8 specimens), **Pompey Complex** (9 specimens), **Frigate Cay** (6 specimens).

These localities include collecting stations 5, 11, 13, 17, 27, 30, 32, 33, 34, 37, 42, 45, 56, 57, 61, 63, 64, 68, 69, 71, 75, 79, 81, 93, 99, 100, 102, 103, 106, 128.

Previous records from Eastern Australia

Low Isles and vicinity, Crossland (1952); **Low Isles**, Stephenson & Wells (1955).

Characters

Coralla are elongate; the length/width ratio averages 2-2.5, and reaches 3 in some specimens. Bigger specimens may have as many as about 1000 septa. Principal septa are conspicuously thicker than the others and distinctly exsert. Their upper margins have large, lobate or subtriangular dentations, often with echinulate or spinose tops and slightly granulated sides (Fig. 287). These granules sometimes fuse in rows parallel to the dentation margins. There are 1 to 5 secondary septa between the primaries, with much smaller or no dentations.

The lower surface is covered with well developed, cylindrical or arborescent spines (Figs. 288, 289) which have spinulose, granulose or echinulate tops. Spines

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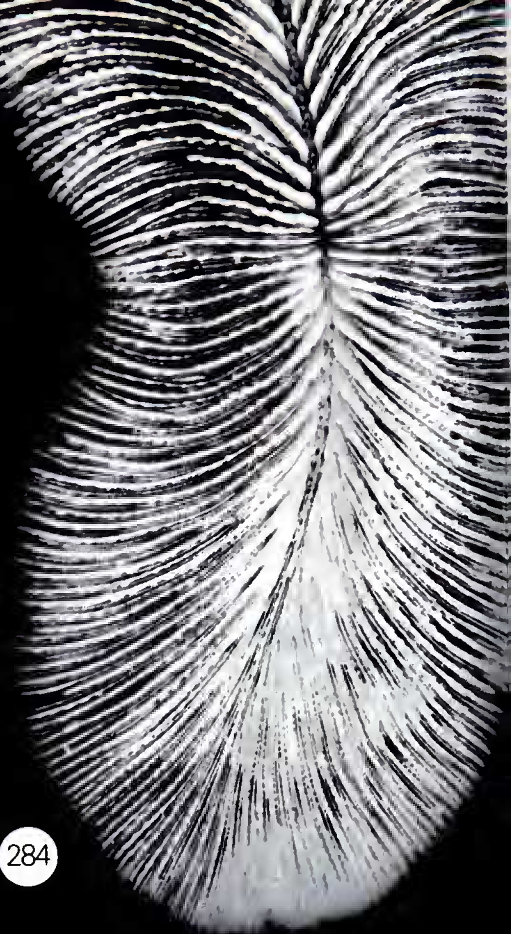

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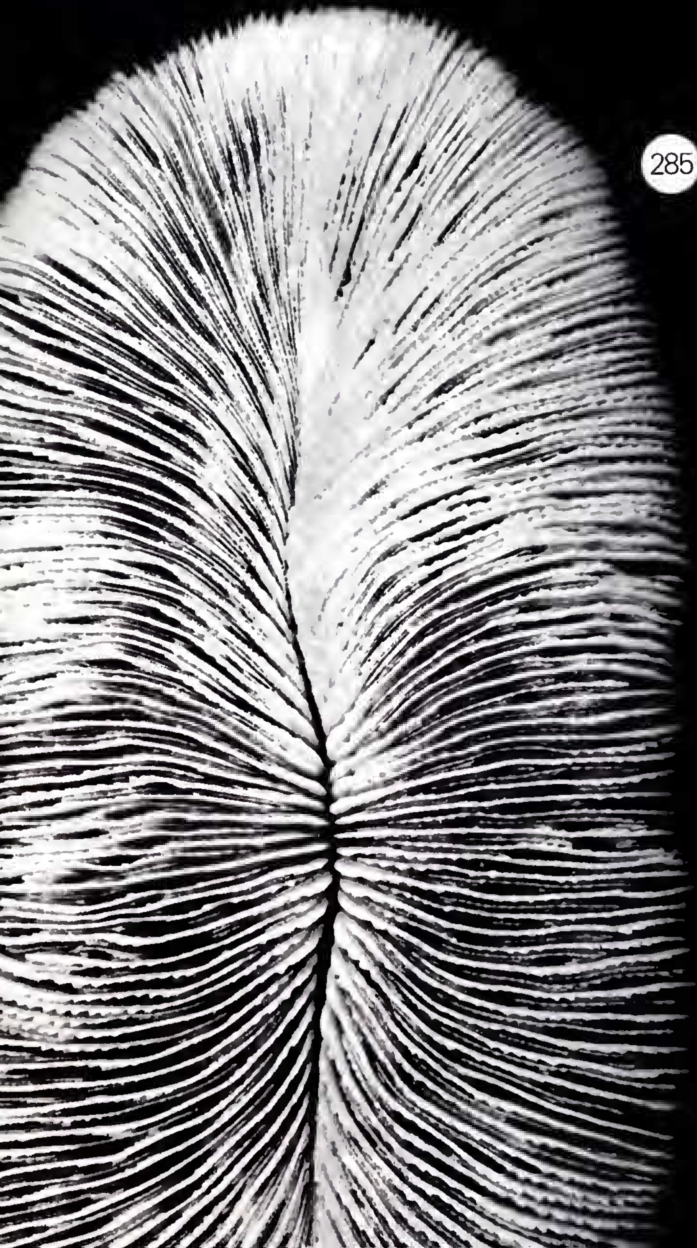

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are arranged in regular rows corresponding to costae although this disposition is sometimes obscured by their proliferation and size. The scar of attachment is visible in juvenile specimens only. Numerous elongate pits are visible near the margins of most specimens.

Skeletal variation

The septal dentations and costal spines are the most constant character of this otherwise highly variable species. Most coralla are slightly arched; some are completely flat, others very arched (up to 10 cm in height). A central constriction in coralla is common, the maximum width to minimum central width ratio reaching 1.4. The ends of coralla are either regularly rounded or slightly tapered (just as with *Herpolitha limax*). The length of the mouth fossa may extend the whole length of the corallum (in which case well defined axial septa may occasionally be present) or be far short of the ends. In two extreme cases, the length of the axial fossa is shorter than the corallum width.

Primary septa may be extremely exsert (up to 7 mm) and distant from each other (up to 8 mm) or hardly any taller than other septa and only characterised by their slightly thicker, larger dentations which vary themselves from nearly smooth to very spinulose or echinulate.

The abundance and development of the spines on the lower face also varies considerably. In some specimens there are only a few rather small spines, generally clearly arranged in rows. This situation, on which Döderlein based his variety *parvispina*, grades towards one in which the spines are very tall, arborescent or not, blunt or conical, covered with granules and which have hirsute spinulations or echinulations at the top. These can be so densely packed that they completely cover the undersurface.

Fungia echinata is normally monostomatous, but may rarely have one, very rarely two, secondary centres in the axial furrow.

Affinities

Fungia brachystoma Thiel, 1932 was based on one juvenile specimen and was described as a new species on the grounds that the mouth fossa is only about half as long as the corallum is wide. The present study indicates that the relative proportions of the various skeletal dimensions have no specific significance in juvenile specimens and it has already been pointed out that the axial furrow may not reach the ends of the corallum. As all other characters of *F. brachystoma* are those of *F. echinata*, it is considered a synonym of *F. echinata*, as already recognised by Umbgrove (1939, 1940) and Scheer & Pillai (1974).

The status of *F. proechinata* remains uncertain. Although included in the '*echinata*' group (i.e. in the subgenus *Ctenactis*) by Döderlein, he himself mentioned that *F. proechinata* comes close to *F. paumotensis* by the granular nature of the ornamentation on the underside. Döderlein's unique specimen was also a juvenile. The mouth fossa is extremely short, as illustrated by Umbgrove (1940), but on that basis alone, *F. proechinata* could not be considered as being different from *F. echinata*.

Distribution

Widespread in the Indo-Pacific, from the Red Sea to Japan and the Society Islands.

Figs. 283-286 *Fungia echinata* (× 0.8).

Fig. 283 From Yorke Island, collecting station 13.
Fig. 284 From the Swain Reefs, collecting station 68.
Fig. 285 From Frigate Cay, Swain Reefs, collecting station 81.
Fig. 286 From Lizard Island, collecting station 32.

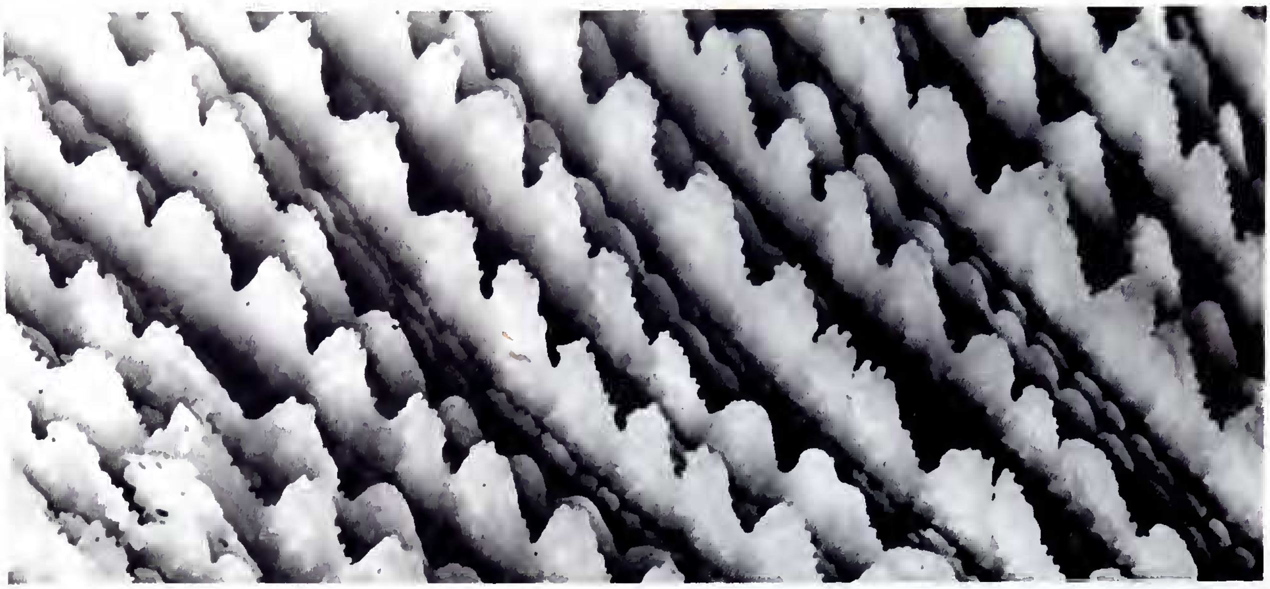


Fig. 287 ▲

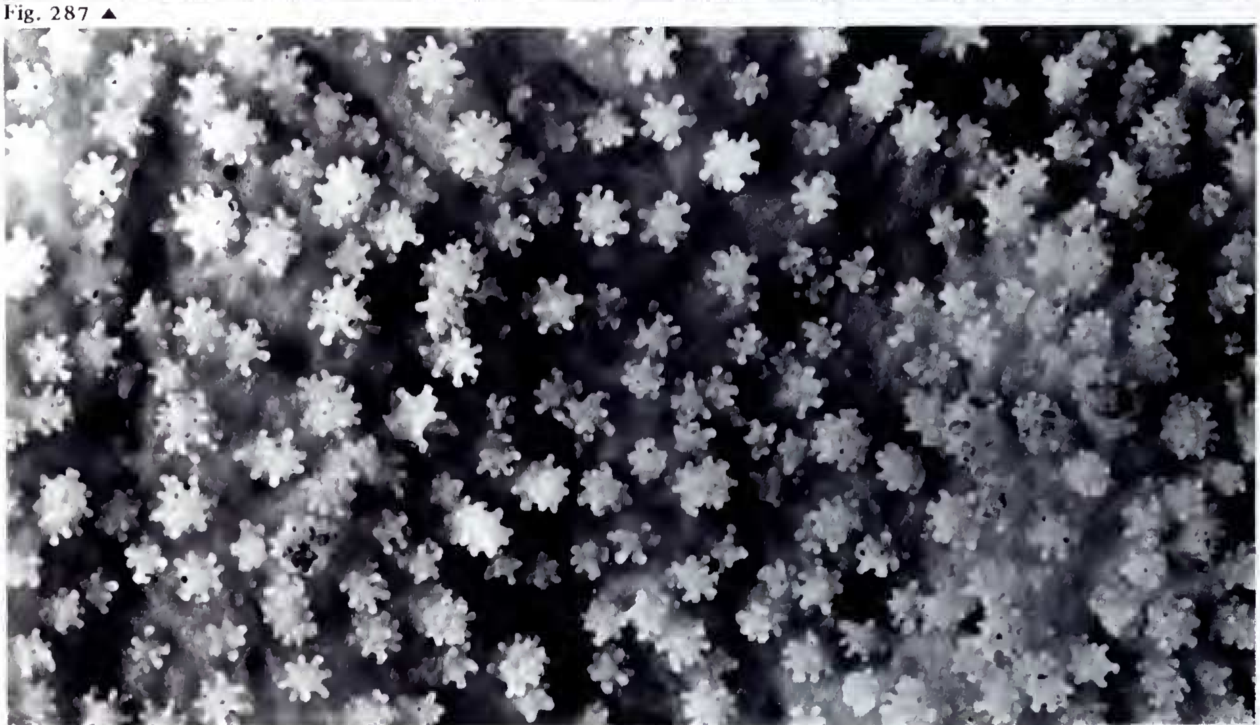


Fig. 288 ▲

Fig. 289 ▼

Generic synonymy

Herpolitha Gardiner, 1905 (*pars*); (*pars*) Boschma (1925).

Fungia (pars); Dana (1846); Gardiner (1909); Matthai (1924); Thiel (1932); Yabe & Sugiyama (1941).

Herpetoglossa Wells, 1966.

Type species *Herpolitha simplex* Gardiner, 1905.

Characters of the genus

Coralla are colonial, free, elongate, concavo-convex. Several centres are developed along the along axis of coralla, in the central furrow. Septal and costal characters are those of *Fungia* (*Ctenactis*) *echinata.*

Introduction

Herpetoglossa is a monospecific genus, homeomorphic with *Herpolitha* and *Fungia* (*Ctenactis*), which is why *H. simplex* has been referred to these two genera by other authors. It comes close to *F.* (*Ctenactis*) *echinata* in its general growth form and septo-costal structures and is probably a recent polystomatous derivative of *Fungia* (*Ctenactis*) just as other polystomatous species tend to derive, in various degrees, from basic monstomatous types throughout the Fungiidae.

Herpetoglossa simplex (Gardiner, 1905)

Synonymy

Fungia crassa Dana, 1846 (*nomen oblitum*).

Herpolitha simplex Gardiner, 1905; Folkeson (1919), Boschma (1925); Nemenzo (1955a); Pillai (1972).

Fungia simplex (Gardiner); Gardiner (1909); Matthai (1924).

Herpetoglossa simplex (Gardiner); Wells (1966).

Fungia echinata (Pallas); *sensu* Matthai (1924, *pars*); *sensu* Thiel (1932, *pars*); *senus* Yabe & Sugiyama (1941, *pars*).

Herpetoglossa simplex has probably often been confused with *Fungia echinata*, but the lack of good figures or accurate descriptions does not allow a full synonymy to be determined. It is likely, however, that in many instances, *Fungia echinata* actually refers to a mixture of *Fungia echinata* and *Herpetoglossa simplex.*

Material studied

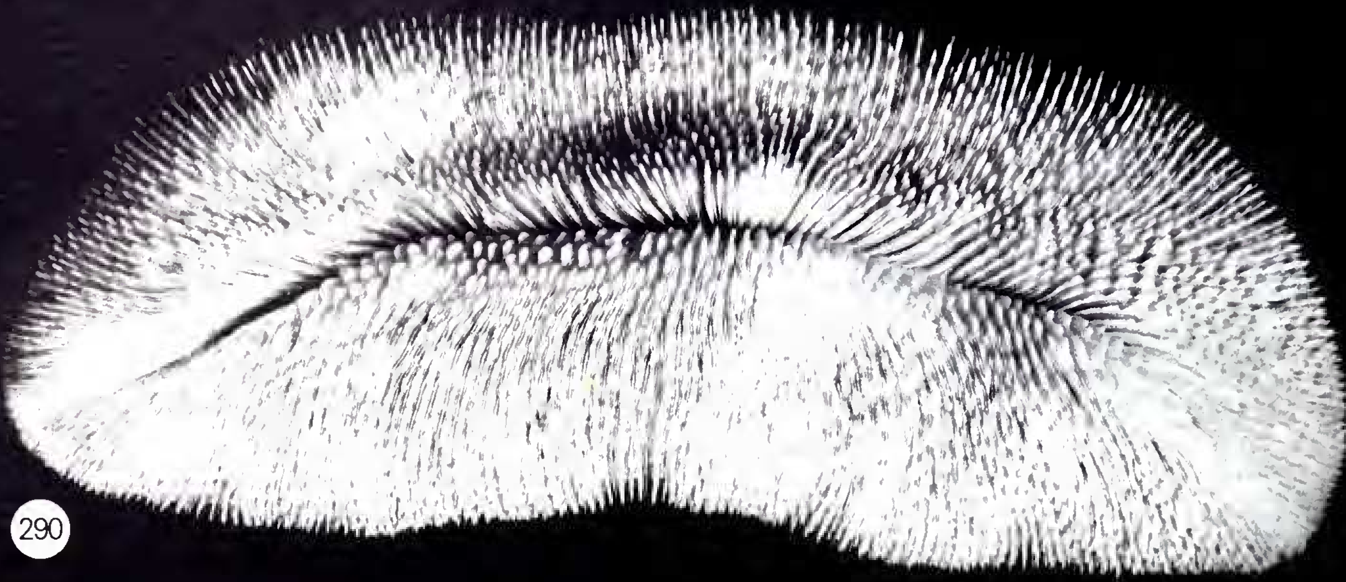
Bramble Cay (2 specimens), **Yorke Island** (2 specimens), **Murray Islands** (2 specimens), **Jewell Reef** (2 specimens), **Nymph Reef, Lizard Island** (14 specimens), **Eyrie Reef, Low Isles** (2 specimens), **Palm Islands** (17 specimens), **Bushy Island-Redbill Reef, Swain Reefs** (2 specimens), **Frigate Cay** (3 specimens).

These localities include collecting stations 11, 13, 20, 30, 32, 33, 34, 35, 37, 42, 45, 55, 56, 58, 59, 61, 69, 75, 79, 81, 87, 89, 90, 100, 128.

Figs. 287-289 *Fungia echinata* (× 5.0).

Figs. 287, 288 From Frigate Cay, same corallum as Fig. 285, showing the appearance of the septa (Fig. 287) and the costal spines (Fig. 288).

Fig. 289 From Lizard Island, same corallum as Fig. 286, showing the costal spines.



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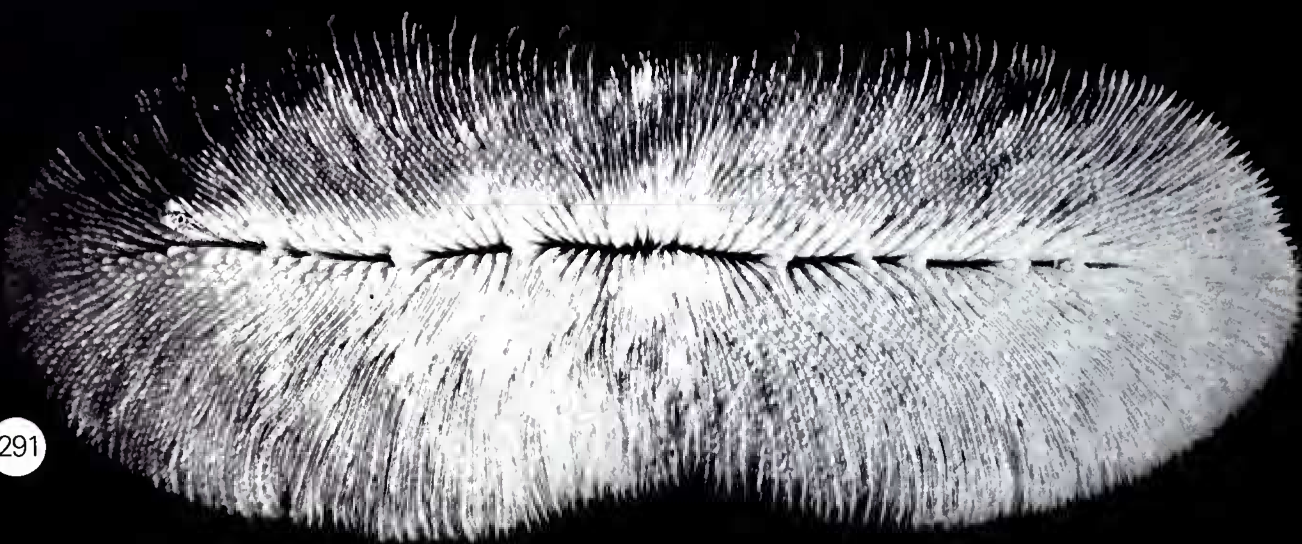

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Previous records from Eastern Australia

Not previously recorded.

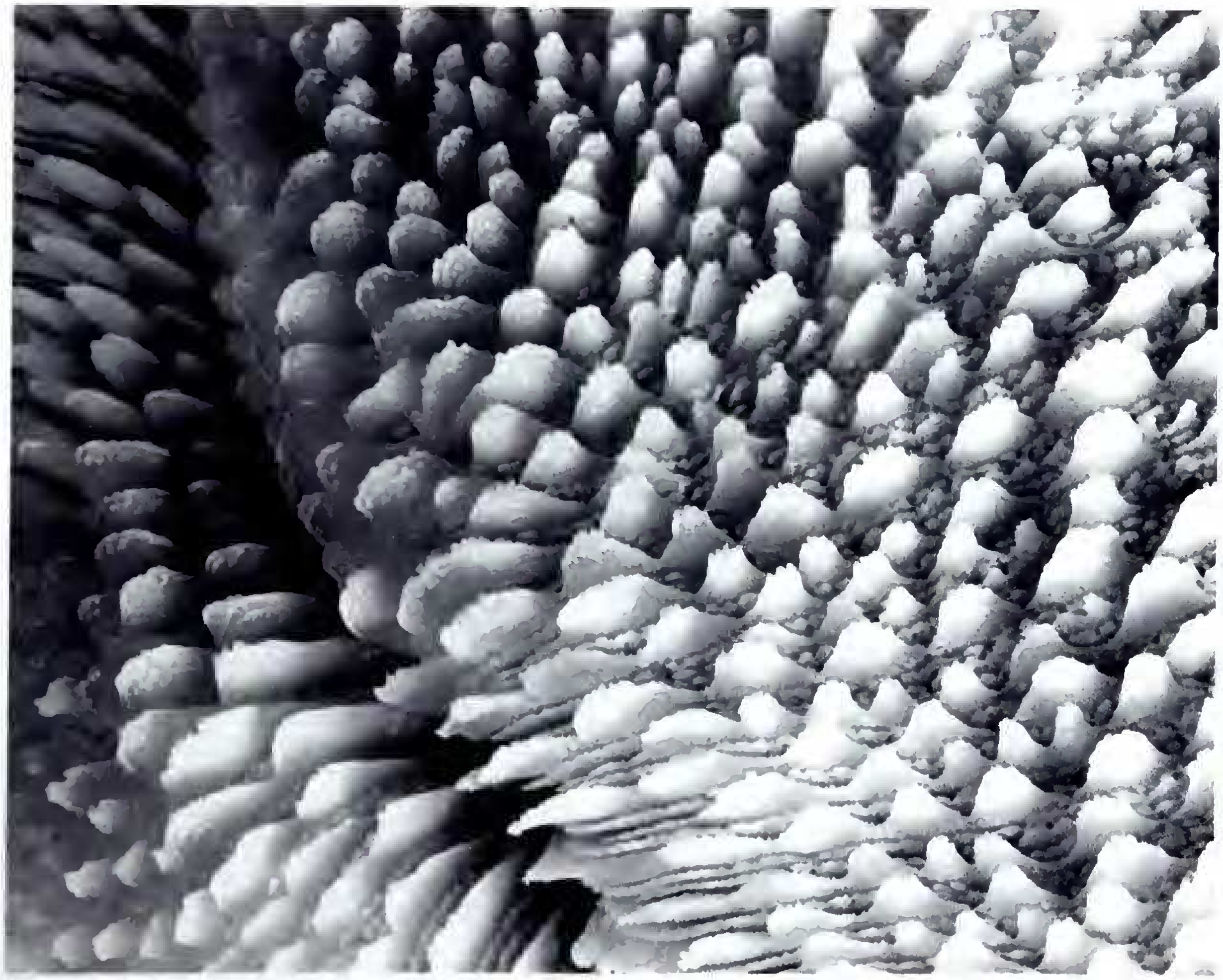
Characters

Coralla are elongate, usually with tips more or less pointed. The length/width ratio varies from 2 to 5 and coralla can be flat or markedly arched. The axial furrow usually extends almost to the corallum tips in small coralla (<15 cm long) where directive septa may be present, but not in larger (particularly arched) specimens. The axial furrow has several centres, except in juvenile stages, which are separated from each other by the fusion of two opposite pairs of septa. There are no secondary (lateral) centres. Septa are numerous, close to each other and markedly alternating in size (Fig. 293). Principal septa, which run uninterrupted from the central fossa to the corallum perimeter, are separated by one or several higher order septa which have large, triangular dentations (<4 mm long). The vertical axis of each dentation is greatly thickened and, viewed from above, the principal septa appear to be composed of a linear series of dilations. The margins of the dentations bear rounded or irregular granules. Secondary septa are thick and porous, even spongiose. Their upper margins are devoid of large dentations, but are irregular and echinulate. Their sides are heavily granulated. Columellar centres are unequally developed and are composed of an elongate mass of anastomosing trabeculae.

Figs. 290-292 *Herpetoglossa simplex* (× 0·5).

Fig. 290 From Iris Point, Orpheus Island, Palm Islands, collecting station 55.
Fig. 291 From Eyrie Reef, collecting station 20.
Fig. 292 From Frigate Cay, Swain Reefs, collecting station 81.
Fig. 293 *Herpetoglossa simplex* from Iris Point, Orpheus Island, same corallum as Fig. 290, showing the appearance of the septa (× 2.5).

Fig. 293 ▼



The undersurface can be perforate, except towards the centre of the corallum, and is covered by numerous, small, compact spines arranged in rows corresponding to costae, except towards the corallum centre, where they become irregular. Spines are ornamented with spinules or small granules.

Herpetoglossa simplex is found mostly on protected or semi-protected reef or lagoon slopes, and on the lagoon floor.

Affinities

Herpetoglossa simplex has been well described and figured by Gardiner (1905) and Boschma (1925). However, more recent authors have confused it with *Fungia* (*Ctenactis*) *echinata* due to a superficial similarity. Adult *H. simplex* are always polycentric, have more numerous, less alternating septa with triangular rather than lobate dentations with a thickened axial rod, and more numerous costal spines.

The generic status of the present species has oscillated between *Herpolitha* (Gardiner, 1905; Boschma, 1925; Nemenzo, 1955a) and *Fungia* (Gardiner, 1909; Matthai, 1924). While recognising that the septo-costal structures are closer to those of *F. echinata*, Boschma (1925) considered that its polycentric condition indicated closer affinity with *Herpolitha* (in particular with *H. weberi*, which has no lateral secondary centres).

Herpetoglossa simplex cannot be included in *Herpolitha* because of its septo-costal structures, nor in *Fungia* because it is polycentric. The establishment of a separate genus by Wells (1966) for this species is therefore entirely justified.

Distribution

Recorded from the Maldive Islands, Indonesia, the Philippines, Palau, the Caroline and Ryūkyū Islands, the Great Barrier Reef, New Caledonia and Fiji.

GENUS *HERPOLITHA* ESCHSCHOLTZ, 1825

Generic synonymy

Fungia Lamarck, 1801 (*pars*).

Herpolitha Eschscholtz, 1825 (*pars*); Klunzinger (1879); Boschma (1925); Vaughan & Wells (1943); Wells (1954, 1956, 1966).

Haliglossa Ehrenberg, 1834 (*pars*).

Herpetolithus Leuckart, 1841; Dana (1846); Verrill (1864).

Herpetolitha Edwards & Haime (1850b, 1851a); Vaughan (1907b, 1918); Matthai (1924).

Type species *Herpolitha limax* (Houttuyn 1772).

Characters of the genus (partly after Vaughan & Wells, 1943 and Wells, 1956)

Coralla are colonial, free, elongate, concavo-convex; budding is intramural, polystomodaeal, producing at first a linear series of centres along the corallum axis. Lateral secondary centres are smaller and less conspicuous than the primary ones; they develop on either side of the axial furrow. Septo-costae are subparallel in mature specimens. Septal and costal characters are *Fungia* (*Pleuractis*)-like. Septal

Figs. 294-297 *Herpolitha limax*, Figs. 294, 295 (× 0.6), Figs. 296, 297 (× 0.4).

Fig. 294 From Esk Island, Palm Islands, collecting station 42.
Fig. 295 From Iris Point, Orpheus Island, Palm Islands, collecting station 55.
Fig. 296 From between Orpheus and Fantome Islands, Palm Islands, collecting station 8.
Fig. 297 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.

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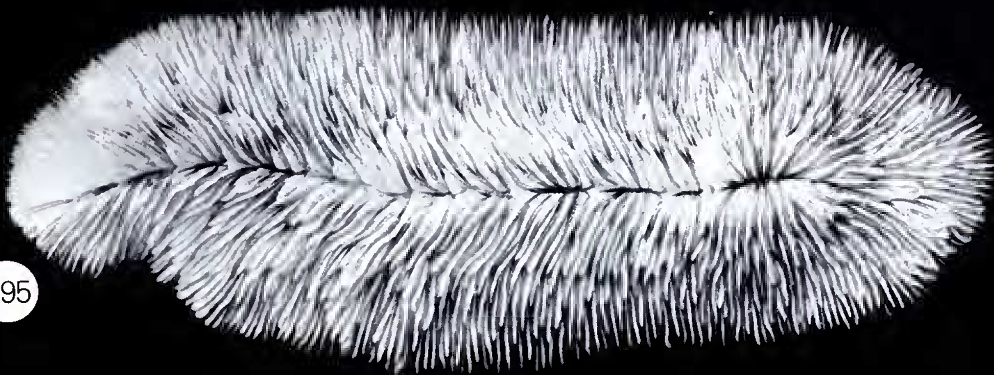

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ornamentation is similar to that of *F.* (*Pleuractis*) *scutaria*. Secondary centres have one, single, tentacle.

Herpolitha limax (Houttuyn, 1772)

Synonymy

Madrepora limax Houttuyn, 1772; Esper (1795).

Madrepora pileus Ellis & Solander, 1786; *non* Linnaeus (1758); *non* Esper (1791).

Fungia limacina Lamarck, 1801; Lamarck (1816); de Blainville (1820, 1830, 1834); Lamouroux (1821).

Fungia limax (Houttuyn); Oken (1815).

Herpolitha limax (Houttuyn); Eschscholtz (1825); Duncan (1889); Gardiner (1909); van der Horst (1921); Boschma (1925, 1929); Crossland (1935, 1952); Umbgrove (1939); Yabe & Sugiyama (1941); Wells (1954); Nemenzo (1955a); Searle (1956); Pichon (1964); Rosen (1971); Scheer & Pillai (1974); Pillai & Scheer (1976).

Haliglossa limacina (Lamarck); Ehrenberg (1834).

Haliglossa interrupta Ehrenberg, 1834.

Haliglossa foliosa Ehrenberg, 1834.

Haliglossa stellaris Ehrenberg, 1834.

Herpetolitha limacina (Lamarck); Leuckart (1841); Dana (1846); Edwards & Haime (1850).

Herpetolithus interrupta (Ehrenberg); Leuckart (1841); Dana (1846).

Herpetolitha foliosa (Ehrenberg); Leuckart (1841); Dana (1846); Vaughan (1907b); Gravier (1911); Matthai (1924).

Herpetolithus stellaris (Ehrenberg); Leuckart (1841); Dana (1846).

Herpetolitha stricta Dana, 1846; Verrill (1864); Vaughan (1918); Matthai (1924).

Herpetolitha crassa Dana, 1846; Quelch (1886); Vaughan (1918).

Herpetolitha limax (Houttuyn); Edwards & Haime (1851a, 1860), Studer (1880); Ortmann (1888, 1889); Bedot (1907); Vaughan (1918); Matthai (1924); Crossland (1931); Thiel (1932).

Herpolitha foliosa (Ehrenberg); Klunzinger (1879); von Marenzeller (1907); Gardiner (1909).

Herpolitha crassa (Dana); Gardiner (1898, 1909).

Herpolitha stricta (Dana); Nemenzo (1955a).

In the above synonymy the spellings *Herpetolithus* and *Herpetolitha* are not separated when applied to the same species name.

Material studied

Warrior Island, Turtle Backed Island, Dungeness Reef, Yorke Island, Great Detached Reef, Howick Island, Jewell Reef (2 specimens), **Lizard Island** (8 specimens), **MacGillivray Reef** (6 specimens), **Ribbon Reef** (3 specimens), **Palm Islands** (27 specimens), **Bait Reef** (2 specimens), **Whitsunday Islands** (11 specimens), **Bushy Island-Redbill Reef, Pompey Complex, Swain Reefs** (5 specimens), **Frigate Cay, Heron Island** (3 specimens).

These localities include collecting stations 1, 13, 32, 34, 37, 41, 42, 45, 55, 60, 63, 65, 71, 74, 76, 79, 80, 81, 89, 92, 93, 97, 98, 99, 100, 102, 121, 123, 138.

Previous records from Eastern Australia

Low Isles (as *H. stricta*) Yonge (1930), (as *Herpolitha*) Stephenson *et al.* (1931), (as *Herpolitha* sp.) Stephenson & Stephenson (1933), (as *Herpolitha*) Moorhouse (1936), Crossland (1952).

Characters and skeletal variation

Coralla are elongate with rounded or pointed tips. The length/width ratio varies from 1.5 to 6. Most specimens are moderately arched, but those with a small length/width ratio are relatively flat (Fig. 298). Regenerated specimens frequently have irregular shapes with up to five ends. Coralla have a linear series of primary centres along the axes with numerous secondary centres on either side. The latter are relatively inconspicuous and are arranged in approximately concentric rows around the axial furrow (Fig. 296). This disposition is often obscured, particularly on larger specimens. Septa are 1-3 cm long and form an irregular series running from one centre to another, almost parallel, in a transverse direction, except towards the corallum ends. Septa originating from the axial furrow never reach the periphery of the corallum in the adult stage. Their margins have a similar ornamentation to that of ***Fungia (Pleuractis)*** with small, regular, triangular dentations, sometimes compressed in a direction perpendicular to the septa. Septal sides bear small granules. Secondary septa alternate with the primaries; they are conspicuously thinner and lower, with irregular, lacerate margins. Columellae are obsolete or absent in secondary centres. They are loosely trabecular and poorly developed in the centres along the axial furrow.

Figs. 298, 299 *Herpolitha limax* (× 0.3).

Fig. 298 From Nara Inlet, Hook Island, same corallum as Fig. 297.
Fig. 299 From between Orpheus and Fantome Islands, same corallum as Fig. 296.


298
299

The lower surfaces of coralla are perforate, except in the central part, and are covered with numerous, small, lightly spinulose or tuberculate spines. These are arranged in well defined rows close to the perimeter of the corallum, but become irregularly distributed in the central part.

Herpolitha limax can be found in most reef biotopes, but is more abundant on protected reef slopes.

Affinities

Herpolitha limax shows a range of growth forms, particularly in the shape of the corallum extremities and in the length of the axial furrow. Variations in the septo-costal structures (crowding and thickness of the septa, size of the septal dentations and costal spines) are continuous from one specimen to another although these have been used to separate different nominal species, particularly by Vaughan (1918), Matthai (1924), and Nemenzo (1955a). Alternatively Edwards & Haime (1860), Ortmann (1888, 1889), van der Horst (1921), Boschma (1925) and Crossland (1952) have considered that *H. limax, H. foliosa, H. stricta* and *H. crassa* are only one species, an opinion now widely accepted.

Despite its variability, *Herpolitha limax* is a conspicuous, easily distinguishable species, with little possibility of confusion with the other species of the genus, except possibly juvenile *H. weberi.*

Distribution

Widely distributed in the Indo-Pacific, from northern Red Sea and Mozambique to Japan and eastern Tuamotu.

Herpolitha weberi (van der Horst, 1921)

Synonymy

Fungia weberi van der Horst, 1921.

Herpolitha weberi (van der Horst); Boschma (1925); Yabe & Sugiyama (1941); Scheer (1974); Pillai & Scheer (1976).

Material studied

Lizard Island (2 specimens), **Eyrie Reef** (2 specimens), **Palm Islands** (15 specimens).

These localities include collecting stations 20, 32, 34, 45, 46, 57, 59, 90, 91, 92, 93.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are elongate, with pointed tips, except where tips have been broken and regenerated. The mean length/width ratio is usually greater than 4 and may be up to 6 (higher than for *H. limax*). Coralla are flat to very arched (with a height equal to or greater than the width), particularly around the axial furrow, which usually reaches the extremities, except when tips are regenerated. Arched coralla are usually thicker than flat ones, particularly in the central part of the corallum. The long axes of coralla

Figs. 300-304 *Herpolitha weberi.*

Figs. 300, 301, 303	Same corallum from Barber Island, Palm Islands, Figs. 300, 301 (× 0.5), Fig. 303 (× 0.3).
Fig. 302	From Eyrie Reef, collecting station 20 (× 1.0).
Fig. 304	Part of the holotype.

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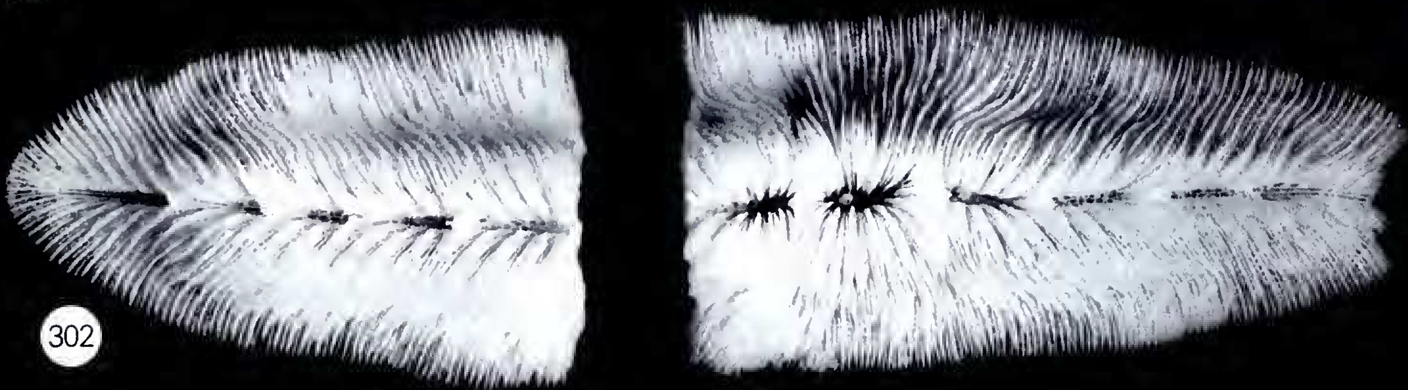

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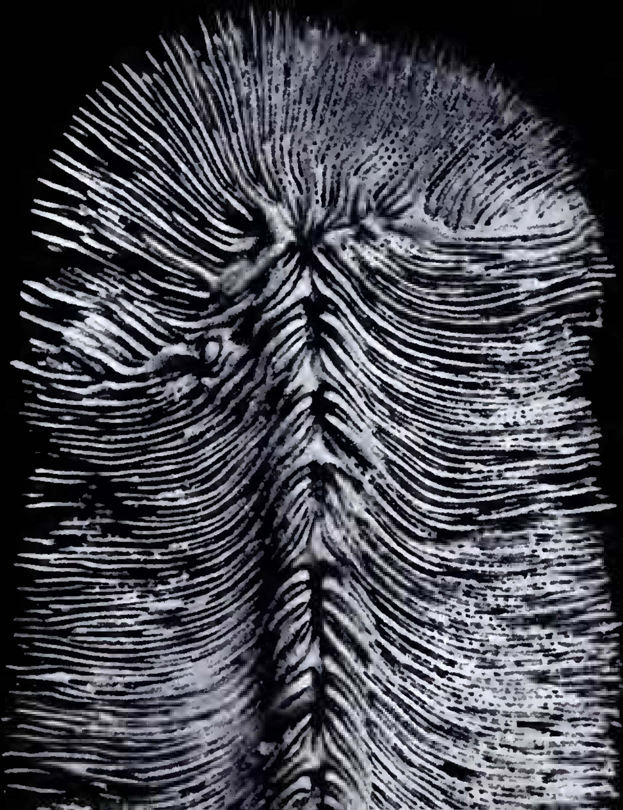

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have a linear series of centres separated by fusion of opposite septa across the axial furrow (Fig. 302). Lateral secondary centres noted by Boschma (1925) are either totally lacking or are very few in number and inconspicuous.

Septa are markedly alternating in height around the axial furrow. They are equal or subequal towards the corallum perimeter. Principal septa run uninterrupted from the axial furrow to the corallum perimeter. Septal margins have numerous, regular, triangular or slightly rounded dentations. Septal sides bear small granules. Columellar centres in the axial furrow are elongate, composed of numerous small papillae. The lower surface is perforate except in the central part and is entirely covered with minute, lightly spinulose spines arranged in rows, which are close to each other and well defined towards the corallum perimeter (Fig. 303). The distribution of costal spines is irregular on the central part.

Herpolitha weberi is found on semi-protected to protected reef slopes.

Affinities

Herpolitha weberi has very similar growth forms and similar septo-costal ornamentations to those of *H. limax*. However, it can be readily distinguished (except possibly in very young stages) by the uninterrupted character of its primary septa (from the axial furrow to the corallum periphery) and by the near absence of lateral secondary centres.

Although only 4 specimens of *H. weberi* are previously recorded, the species appears to display little intraspecific variability. Variation is mostly in the corallum shape (arched or flat with sharp or rounded ends). Pillai & Scheer (1976) noted that the septa of their only specimen alternate at the growing corallum periphery, a character not found in the present series.

In their account of *H. weberi*, Yabe & Sugiyama (1941) wrote that 'in almost all the species of *Fungia* previously described, the septa of older cycles as a rule extend to the margins, while in *Herpolitha*, this is not the case. *H. weberi* differs from *Fungia* in this respect, and evidently belongs to *Herpolitha*'. Although this generic position is correct, these reasons for it are not, for all specimens referred to *H. weberi*, including Yabe & Sugiyama's, have most, if not all principal septa extending from the axial furrow to the corallum perimeter. Justifications for including van der Horst's *F. weberi* in *Herpolitha* are in the constantly colonial nature of the corallum and in the close similarities of the costal and septal ornamentation with *H. limax*.

Distribution

Recorded from the Maldive Islands, the Banda Sea (Paternoster Islands), Palau, and the Great Barrier Reef.

GENUS *POLYPHYLLIA* QUOY & GAIMARD, 1833

Generic synonymy

Fungia Lamarck, 1801 (*pars*); (*pars*) Oken (1815); (*pars*) Lamarck (1816); Lamouroux (1824); de Blainville (1820, 1830, 1834).

Agaricia Schweigger, 1820 (*pars*).

Herpolitha Eschscholtz, 1825 (*pars*).

Polyphyllia Quoy & Gaimard, 1833; Dana (1846); Edwards & Haime (1849c); Boschma (1925); Vaughan & Wells (1943); Wells (1966).

Lithactinia Lesson, 1832.

Cryptabacia Edwards & Haime, 1849c.

Type species *Polyphyllia talpina* (Lamarck, 1801).

Characters of the genus

Coralla are polystomatous, concavo-convex, mostly elliptical or elongate in outline. Colony formation is by linear polystomodeal budding in early stages, followed by abundant circumoral budding. Secondary centres are numerous and equal or nearly equal in size to those of the axial furrow, which may become obscure. Septal and costal characters are those of *Fungia* (*Pleuractis*) *paumotensis* and *Herpolitha*.

Introduction

The three genera *Cryptabacia*, *Polyphyllia* and *Lithactinia* were considered as distinct by Edwards & Haime (1860) on the basis of differences between primary centres (of the axial furrow) and secondary centres and on the more or less radiating arrangement of the septal lamellae:

Cryptabacia: Axial furrow with a conspicuous linear series of primary centres. All centres show clearly radiating septal lamellae.

Polyphyllia: A central series of corallites is present. Radiating arrangement of septal lamellae is inconspicuous in primary centres, and totally absent in secondary centres.

Lithactinia: Axial furrow is absent. No differentiation between primary and secondary centres. No radiating arrangement of the septal lamellae. Centres themselves are indistinct.

Edwards & Haime noted the close affinities of these genera: 'Ce petit groupe (*Polyphyllia*), dans les limites que nous lui assignons ici fait le passage des Cryptabacies aux Lithactinies'. Coralla characterising each nominal genus are not uncommon, although large suites of specimens clearly show that only a single species is involved.

Polyphyllia talpina (Lamarck, 1801)

Synonymy

Fungia talpina Lamarck, 1801; Lamarck (1816).

Fungia talpa Oken, 1815; de Blainville (1820); Lamouroux (1824).

Agaricia talpa (Oken); Schweigger (1820).

Herpolitha talpa (Oken); Eschscholtz (1825).

Polyphyllia talpa (Oken); de Blainville (1830, 1834); Ehrenberg (1834); Dana (1846); Ortmann (1888).

Polyphyllia substellata de Blainville, 1830; de Blainville (1834); Edwards & Haime (1851a, 1860).

Lithactinia novaehiberniae Lesson, 1832; Dana (1846); Edwards & Haime (1851a, 1860).

Polyphyllia pelvis Quoy & Gaimard, 1833; Dana (1846); Edwards & Haime (1851a, 1860).

Polyphyllia sigmoides Ehrenberg, 1832; Dana (1846).

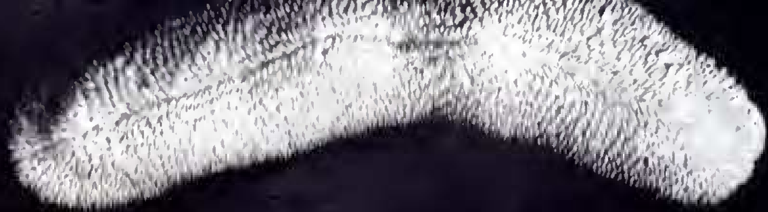
Polyphyllia leptophylla Ehrenberg, 1832; Dana (1846).

Polyphyllia pileiformis Dana, 1846.

Polyphyllia galeriformis Dana, 1846.

Cryptabacia talpa (Oken); Edwards & Haime (1850b).

Cryptabacia talpina (Lamarck); Edwards & Haime (1851a, 1860); Verrill (1864);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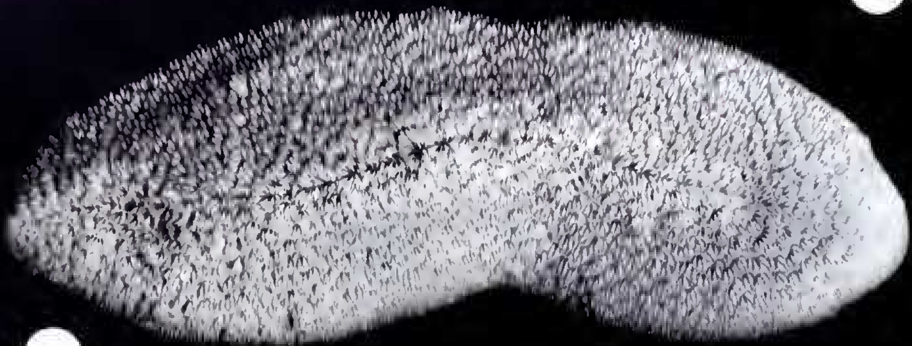
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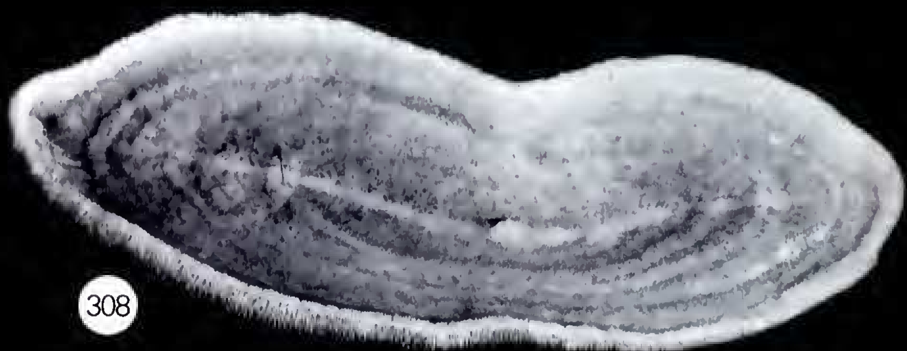
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Studer (1880); Duncan (1889); Quelch (1886); Bedot (1907).

Cryptabacia leptophylla (Ehrenberg); Edwards & Haime (1851a, 1860).

Lithactinia pileiformis (Dana); Quelch (1886); Ortmann (1888).

Lithactinia galeriformis (Dana); Quelch (1886); Vaughan (1905).

Polyphyllia talpina (Lamarck); Gardiner (1909); Vaughan (1918); van der Horst (1921); Boschma (1925); Faustino (1927); Thiel (1932); Eguchi (1938); Umbgrove (1939); Yabe & Sugiyama (1941); Crossland (1952); Nemenzo (1955a); Searle (1956); Wells (1966); Wells & Davies (1966); Scheer & Pillai (1974); Pillai & Scheer (1976).

Polyphyllia producta Folkeson, 1919.

Polyphyllia novaehiberniae (Lesson); Matthai (1924).

Material studied

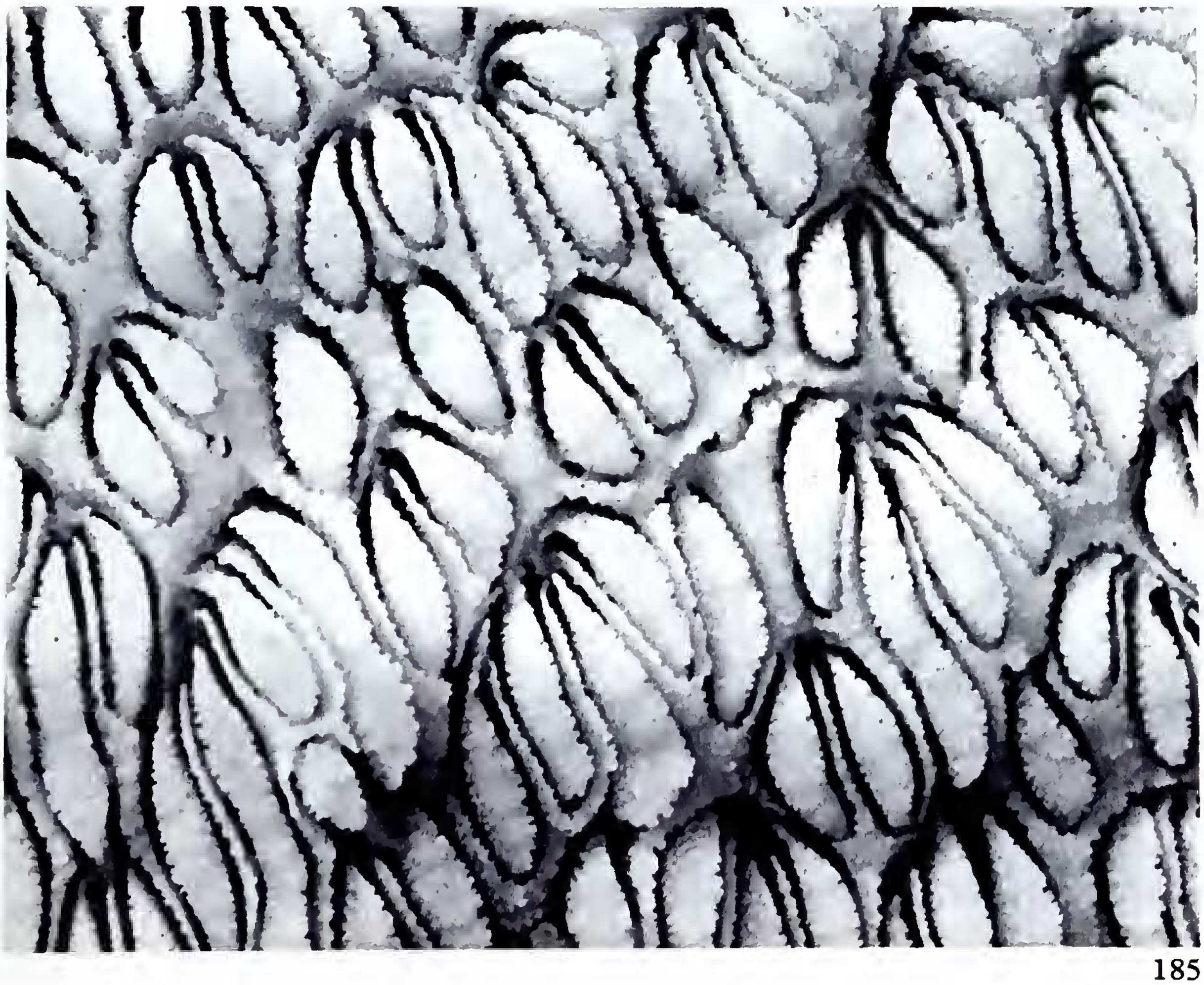
Yorke Island, Murray Islands, Lizard Island (4 specimens), **Ribbon Reef, Hope Island** (4 specimens), **Palm Islands** (11 specimens), **Magnetic Island, Whitsunday Islands** (2 specimens), **Bushy Island-Redbill Reef, Pompey Complex, Swain Reefs** (3 specimens).

These localities include collecting stations 67, 68, 73, 76, 79, 116.

Figs. 305-309 *Polyphyllia talpina* (× 0.5).

Figs. 305, 306 From Hope Island.
Figs. 307, 308 From the Swain Reefs, collecting station 69.
Fig. 309 From Magnetic Island.

Fig. 310 *Polyphyllia talpina* from the Swain Reefs, same corallum as Figs. 307, 308 (× 5.0).



Previous records from Eastern Australia

Murray Islands, Vaughan (1918); **Low Isles,** Crossland (1952).

Characters and skeletal variations

Coralla are generally elongate, often irregular in outline, flat or strongly arched, sometimes discoidal or branched. There is usually an axial furrow containing centres arranged in series which reaches the extremities in flat coralla, but it falls short of the extremities in arched ones. Where an axial furrow is present, the central corallite is sometimes distinguishable. Centres are numerous and, except for the axial row, are arranged without definite pattern.

Principal septa are short, thick lamellae, elliptical in outline, sometimes petaloid. Short septa have rounded or lobate margins; longer septa have flat margins. The arrangement of the principal septal lamellae is very variable. They can be disposed radially over the whole upper surface except for the periphery, or the radial pattern may be present only along the axis of the corallum with parallel septa over the rest of the upper surface arranged perpendicular to the perimeter. Principal septa have triangular dentations, sometimes compressed transversely, and all septal margins and dentations bear small conical spinules or rounded granules.

Secondary septa are markedly lower than the principal septa. They are either very thin, or can be as thick as the primary septa. They regularly fuse together in front of the principal septa, which therefore appear to be individually enclosed within an extensive skeletal network covering the whole upper surface of the corallum. When principal septa are clearly radially arranged, the reticulate pattern arising from the fusion of secondary septa is less conspicous, but still gives the corallum its characteristic appearance (Fig. 310).

The undersurface is perforated almost to the centre. It is covered with numerous, very small spines with blunt tips and bearing small conical spinules or rounded granules. A linear arrangement of the spines, corresponding to costae, can sometimes be seen, at least on the outer half of the undersurface.

Polyphyllia talpina is mostly found on protected slopes and lagoon floors, often on muddy substrates.

Affinities

The intraspecific variability of *P. talpina* is such that early authors described it as eight different species of three different genera, *Polyphyllia*, *Cryptabacia* and *Lithactinia*, later to be synonymised by Gardiner (1909). Although van der Horst (1921) recognised *P. pileiformis* and *P. galeriformis* and Matthai (1924) *P. novaehiberniae* as species distinct from *P. talpina*, it is now widely agreed that these are synonyms. Similarly, *P. producta* Folkeson, 1919 is not specifically different from *P. talpina*.

Distribution

Recorded from Madagascar, Mauritius, the Maldive and Nicobar Islands, Indonesia, the Philippines, the Ryūkū Islands, Palau, the Great Barrier Reef, Fiji and Tonga.

GENUS *HALOMITRA* DANA, 1846

Generic synonymy

Madrepora (*pars*); Linnaeus (1758); Pallas (1766).

Fungia (*pars*); Lamarck (1801); de Blainville (1820, 1830, 1834); Lamouroux (1824).

Halomitra Dana, 1846; Edwards & Haime (1851a); (*pars*) Boschma (1925); Vaughan & Wells (1943); Matthai (1948a); Wells (1966).

Type species *Halomitra pileus* (Linnaeus, 1758)

Characters of the genus (partly after Wells, 1966)

Coralla are polycentric, free, subcircular, gently convex or strongly arched (bell-shaped), without an axial furrow. Colony formation is by circumoral, polycyclic polystomodeal budding. Septo-costal characters are those of *Fungia (Fungia) fungites.*

Halomitra is homeomorphic with *Sandalolitha* and *Zoopilus*, particularly with the latter (not recorded from Eastern Australia). *Halomitra* and *Zoopilus* can be readily distinguished by the characters of their septo-costal structures, which are *Fungia (Ctenactis) echinata*-like in *Zoopilus.*

Halomitra pileus (Linnaeus, 1758)

Synonymy

Madrepora pileus Linnaeus, 1758; Pallas (1766); Linnaeus (1767).

Fungia pileus (Linnaeus); Lamarck (1801, 1816); de Blainville (1820, 1830, 1834); Lamouroux (1824).

Halomitra pileus (Linnaeus); Dana (1846); Edwards & Haime (1851a, 1860); Ortmann (1888); Studer (1901); van der Horst (1921); Boschma (1959).

Halomitra clypeus Verrill, 1864.

Halomitra tiara Verrill, 1864; Quelch (1886); Studer (1901); van der Horst (1921); Faustino (1927).

Halomitra concentrica Studer, 1901; Faustino (1927).

Halomitra philippinensis Studer, 1901; Gardiner (1905); Vaughan (1905); Boschma (1925); Faustino (1927); Thiel (1932); Eguchi (1938); Yabe & Sugiyama (1941); Wells (1954); Nemenzo (1955a); Pichon (1964); Wells & Davies (1966); Rosen (1971); Pillai & Scheer (1976).

Halomitra louwiniae van der Horst, 1921; Scheer (1972).

non Halomitra fungites Studer, 1901 (= *Fungia fungites*)

Material studied

Anchor Cay (2 specimens), **Murray Islands** (7 specimens), **Ashmore Reef, Great Detached Reef, Tijou Reef** (2 specimens), **Jewell Reef** (6 specimens), **Low Isles, Yule Reef, Gould Reef, Bushy Island-Redbill Reef, Pompey Complex** (7 specimens), **Frigate Cay** (4 specimens), **Swain Reefs.**

These localities include collecting stations 2, 5, 7, 27, 61, 69, 71, 75, 80, 81, 106, 113, 129.

Previous records from Eastern Australia

Torres Strait, Wells (1955a).

Characters

Coralla are circular, discoidal or contorted, almost flat to very arched (dome or bell-shaped, Fig. 311), sometimes higher than they are wide. They are up to 60 cm diameter and are usually 10-15 mm (rarely 30 mm) thick. A central corallite is usually distinguishable, although these are not always larger than the secondary corallites. The latter are either few in number, inconspicuous and scattered over the upper surface, or numerous and arranged in more or less regular, concentric rows. Central corallites are usually radially symmetrical. The development of primary septa is variable and largely depends on the number of secondary centres. Where these are numerous, septa are short lamellae connecting one centre to another, their extrem-

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ities curving towards the centres. Where they are sparse, most primary septa run uninterrupted from the central corallite to the corallum periphery. Secondary septa strongly alternate in height with the primary septa. Synapticulae connecting the lateral sides of the septa are clearly visible. Primary septa have well developed triangular dentations up to 3 mm high and slightly thickened in a trabecular direction at the apex. The undersurface is perforate, sometimes only in the marginal part. Costae are low and arranged radially from the centre to the perimeter. They have tall, conical spines, up to 4 mm high, with smooth sides and spinulose tips.

Septo-costal structures are in every respect similar to those of *Fungia fungites*.

Colonies frequently have brightly coloured margins, usually pink or purple. They are found on semi-exposed to protected, mid and lower reef and lagoon slopes, amongst other corals, or on soft, sometimes muddy substrates.

Affinities

There is little doubt that the six nominal species of *Halomitra* are one species, as indicated by Boschma (1925). Boschma originally retained Studer's name *H. philippinensis*, but more recently (1959) reinstated Linnaeus' name *pileus*, with the implication that *Halomitra* is a monospecific genus. Wells (1966), however, recognised two species. Boschma (1925) also includes *Zoopilus echinatus* in *Halomitra* but *Zoopilus* clearly has *Fungia* (*Ctenactis*)-like septo-costal structures.

Distribution

Recorded from Madagascar, Chagos, the Maldive Islands, Indonesia, the Philippines, Palau, the Great Barrier Reef, the Solomon and Marshall Islands, Fiji and Samoa. The species is also reported from Hawaii by Thiel (1932) but this has not been confirmed (Maragos, 1972, 1977).

GENUS *SANDALOLITHA* QUELCH, 1884

Generic synonymy

Sandalolitha Quelch, 1884.

Podabacia (Edwards & Haime); (*pars*) Quelch (1886); (*pars*) Studer (1901); *non* Edwards & Haime (1849c).

Halomitra (Dana); Gardiner, 1898; (*pars*) Studer (1901) (Subgenus *Podabacia*); (*pars*) Boschma (1925); (*pars*) Thiel (1932); *non* Dana (1846).

Doederleinia Gardiner, 1909; van der Horst (1921); Wells (1936); Matthai (1948).

Parahalomitra Wells, 1937; Vaughan & Wells (1943); Wells (1966).

Fungia (*pars*) Vaughan & Wells (1943); *non Fungia* Lamarck, 1801.

Type species *Sandalolitha dentata* Quelch, 1884

Characters of the genus

Coralla are polycentric, free, without an axial furrow. Colony formation is by repeated circumoral followed by marginal budding. Septo-costal characters are those of *Fungia* (*Verrillofungia*).

Although homeomorphic with *Halomitra*, coralla of *Sandalolitha* are generally more irregular, elongate and more heavily calcified. These genera have repeatedly been confused, although their septo-costae structures are distinct.

Figs. 311-314 *Halomitra pileus* (× 0.7).

Figs. 311, 312 From Frigate Cay, Swain Reefs, collecting station 81.
Figs. 313, 314 Same corallum from the Pompey Complex, collecting station 71.

Wells (1937) established the genus *Parahalomitra* for species of *Doederleinia* Gardiner, 1909 which is preoccupied (Steindachner, 1883). Later (1954, 1966) he drew attention to similarities between *Parahalomitra* and *Sandalolitha* and examination of Quelch's type shows that *Parahalomitra* has the same septo-costal structures as *Sandalolitha*, the latter being distinguished only by having relatively few secondary centres, a situation not uncommon in colonial free-living fungiids (e.g. in *Halomitra pileus* and *Zoopilus echinatus*). The type specimen of *Sandalolitha dentata* Quelch comes from Tahiti, a marginal belt, where some morphological deviation from the normal western Pacific range of variation might be expected. *Sandalolitha* is therefore considered a senior synonym of *Parahalomitra*, as previously concluded by Mergner & Scheer (1974) and Pillai & Scheer (1976).

Sandalolitha robusta (Quelch, 1886)

Synonymy

Podabacia robusta Quelch, 1886; Bedot (1907); Matthai (1923a).

Halomitra irregularis Gardiner, 1898; Studer (1901).

Halomitra robusta (Quelch); Studer (1901); Boschma (1925, 1929); Thiel (1932); Umbgrove (1939, 1940); Yabe & Sugiyama (1941), Crossland (1952).

Doederleinia robusta (Quelch); Gardiner (1909); van der Horst (1921).

Doederleinia irregularis (Gardiner); Gardiner (1909); van der Horst (1921); Wells (1936).

Doederleinia sluiteri van der Horst, 1921.

Parahalomitra irregularis (Gardiner); Wells (1937); Nemenzo (1955a).

Parahalomitra robusta (Quelch); Wells (1954); Nemenzo (1955a); Stephenson & Wells (1955).

Sandalolitha robusta (Quelch); Mergner & Scheer (1974); Pillai & Scheer (1976).

The relationships of *S. robusta* with the type species of the genus, *S. dentata* Quelch, remain uncertain; the two nominal species show similar septo-costal structures, but *S. dentata* has relatively few secondary centres.

The present authors agree with Wells (1954) and Pillai and Scheer (1976), that the two species should remain distinct until variation in mature *S. dentata* (preferably at its type locality) is established. If synonymised, the name *dentata* would have priority.

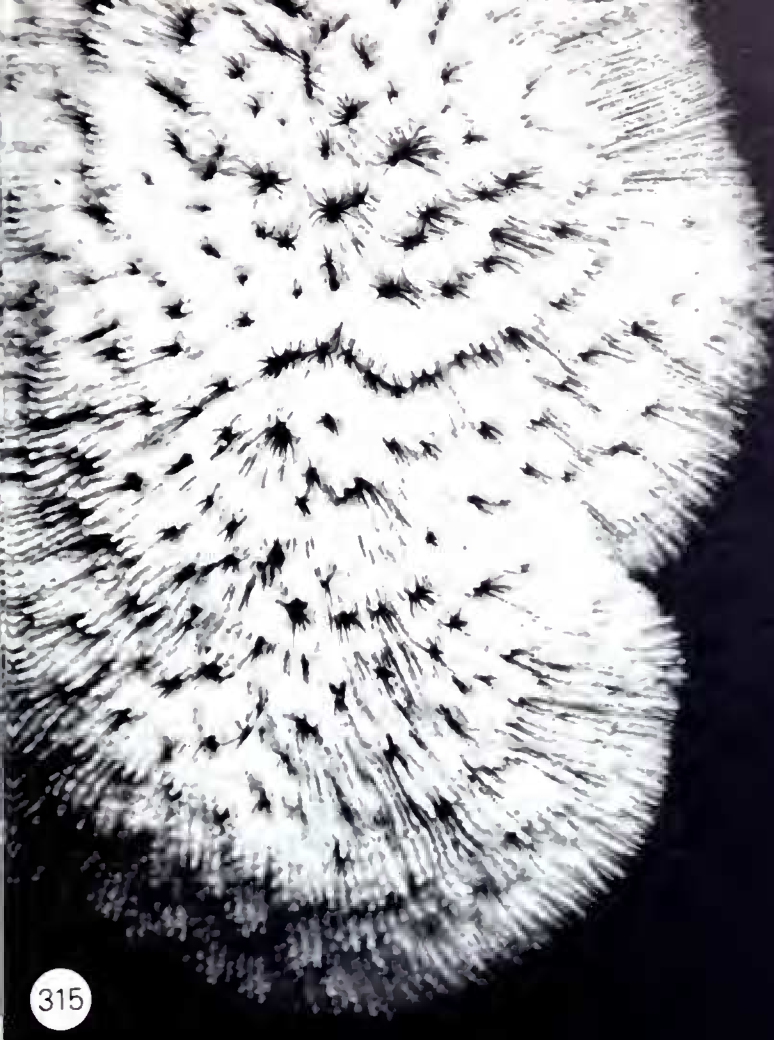
Material studied

Bramble Cay (3 specimens), **Yorke Island, Murray Islands** (11 specimens), **Turtle Backed Island** (2 specimens), **Great Detached Reef, Tijou Reef** (3 specimens), **Jewell Reef** (2 specimens), **Bewick Island, Lizard Island** (16 specimens), **MacGillivray Reef, Ribbon Reef** (3 specimens), **Plug Reef, Hope Island** (2 specimens), **Low Isles** (4 specimens), **Palm Islands** (9 specimens), **Parker Reef, Whitsunday Islands** (2 specimens), **Bushy Island-Redbill Reef, Pompey Complex** (2 specimens), **Frigate Cay, Swain Reefs** (4 specimens), **Wistari Reef.**

These localities include collecting stations 1, 2, 7, 11, 12, 13, 18, 27, 28, 29, 32, 33, 34, 41, 42, 55, 56, 61, 63, 64, 65, 69, 70, 71, 74, 80, 81, 96, 98, 99, 100, 109, 117, 127, 128, 138.

Figs. 315-318 *Sandalolitha robusta* (× 0.9).

Figs. 315, 317 Same corallum from Ribbon Reef, collecting station 63.
Figs. 316, 318 Same corallum from Lizard Island, collecting station 11.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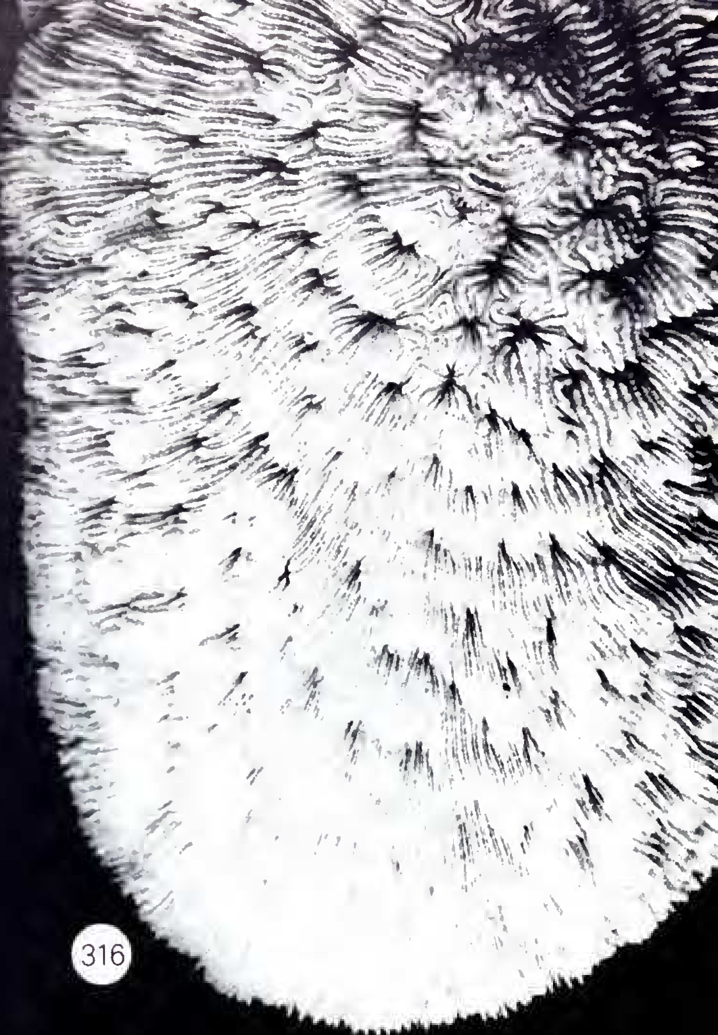
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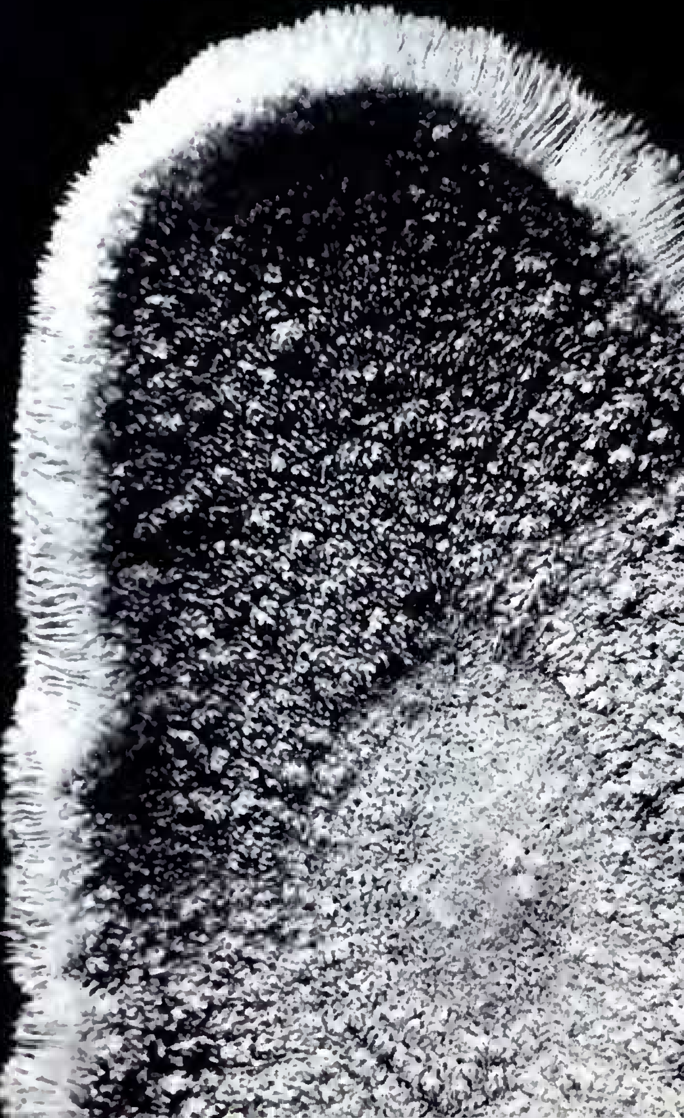
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Previous records from Eastern Australia

Low Isles (as *Doederleinia irregularis*) Stephenson & Stephenson (1933), (as *Halomitra*) Manton (1935), (as *Parahalomitra robusta*) Stephenson & Wells (1955).

Fig. 319 *Sandalolitha robusta* from Dewar Island, Murray Islands, collecting station 29 (× 2.5).
Fig. 320 Holotype of *Sandalolitha robusta* (× 1.0).

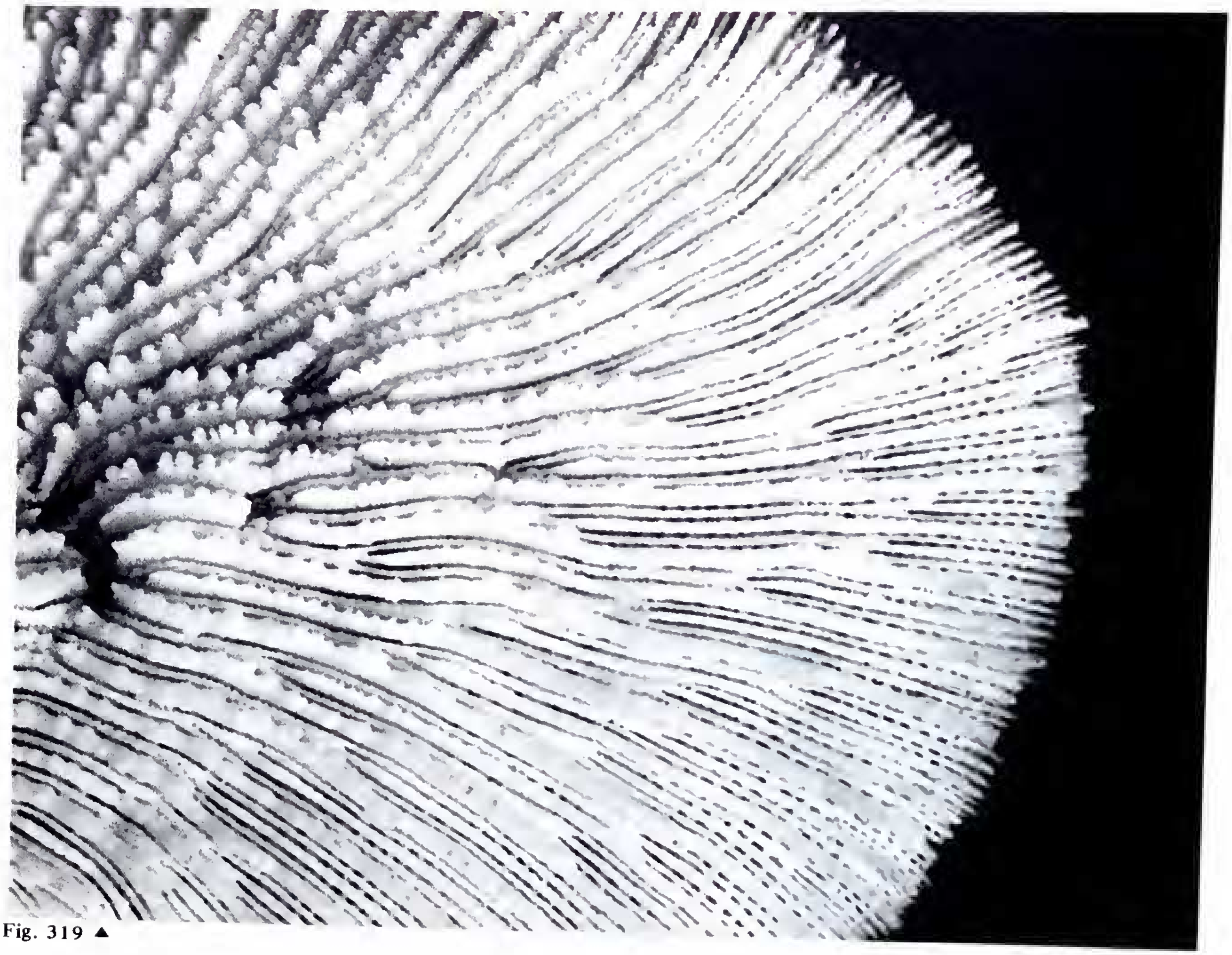
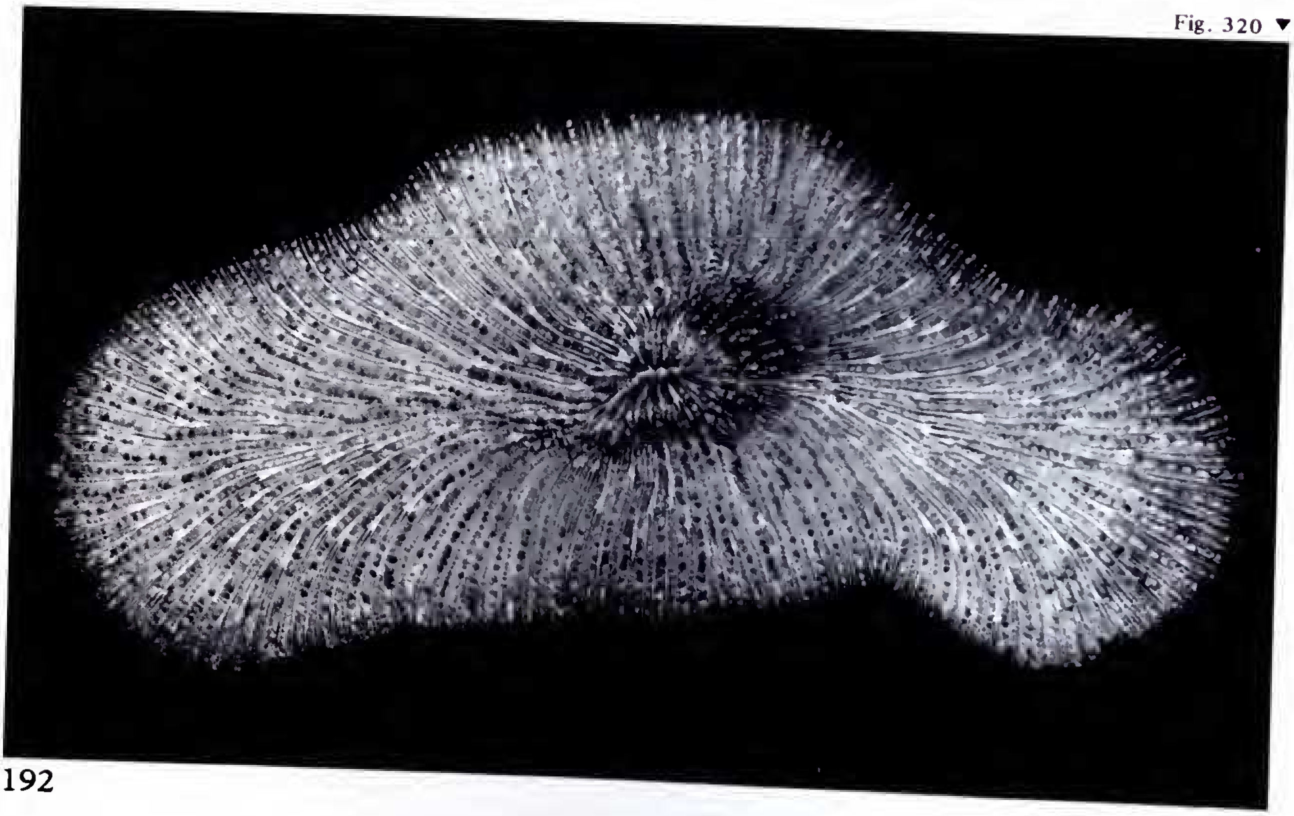


Fig. 319 ▲

Fig. 320 ▼



Characters and skeletal variation

Coralla are polycentric, without an axial furrow, rounded to elongate, usually irregular in outline, almost flat to dome-shaped. They are up to 50 cm long and up to 30 mm thick, particularly where the central part is strongly arched. The central corallite is not always distinct, but is usually so in small specimens. Secondary corallites, originating from circumoral budding, may be few in number and localised in the central part of the corallum, or numerous and irregularly distributed over the entire upper surface. Septa are of variable length; they run from one centre to the next, or from one centre to the corallum perimeter. Juvenile coralla have septa radiating from the central corallite; in mature coralla, the arrangement is irregular, with septa more or less radiating from every secondary centre, or even tending towards a thamnasteroid pattern. Principal septa (Fig. 319) are thick and alternate with lower, thinner, secondary septa which have finely dentate margins. The margins of principal septa have *Fungia* (*Verrillofungia*)-like dentations up to 2 mm high, with rounded or flat tops. These dentations are covered (on both margins and sides) with numerous blunt granules. Columellar centres are irregularly developed, varying from rudimentary to clearly visible and papillose. The undersurface is covered with numerous spines, club-shaped or ramose, with blunt tips and bearing irregular granules. In some coralla, spines are arranged in distinct rows corresponding to costae, in others the costae remain indistinct and spines are without definite arrangement. The undersurface is perforate in juvenile stages; mature coralla have perforations mostly restricted to the perimeter, or they may be completely lacking in large, thick specimens.

Distribution

Recorded from the Maldive and Minicoy Islands, Indonesia, the Philippines, Palau, the Caroline Islands, the Great Barrier Reef, New Caledonia, Fiji, the Marshall Islands and the Tuamotu Archipelago.

GENUS *LITHOPHYLLON* REHBERG, 1892

Generic synonymy

Lithophyllon Rehberg, 1892; Vaughan & Wells (1943); Wells (1956).

Podabacia; (*pars*) Verrill (1901); van der Horst (1921).

Type species *Lithophyllon undulatum* Rehberg, 1892 (= *Leptoseris edwardsi* Rousseau, 1854).

Characters of the genus

Coralla are polycentric, explanate, foliaceous, unifacial and remain attached to the substratum in the adult stage. Colony formation is by marginal budding. Septo-costal structures are those of *Cycloseris*.

Lithophyllon is a little known genus and has often been overlooked, notably by van der Horst and Yabe *et al.* (1936) who ascribed several nominal species of *Lithophyllon* to its homeormorph *Podabacia*. This confusion largely results from Rousseau's (1854) and Edwards & Haime's (1860) inclusion of *edwardsi* in the genus *Leptoseris* as well as a lack of any diagnosis or description by Rehberg (1892) for *Lithophyllon undulatum*.

Despite superficial similarity, the two genera can readily be distinguished on the basis of growth form and septo-costal structures. *Podabacia* is essentially laminar, either flat or cup-shaped and septo-costal structures are those of *Fungia* (*Verrillofungia*). *Lithophyllon* has an initially encrusting, then foliate growth form with large

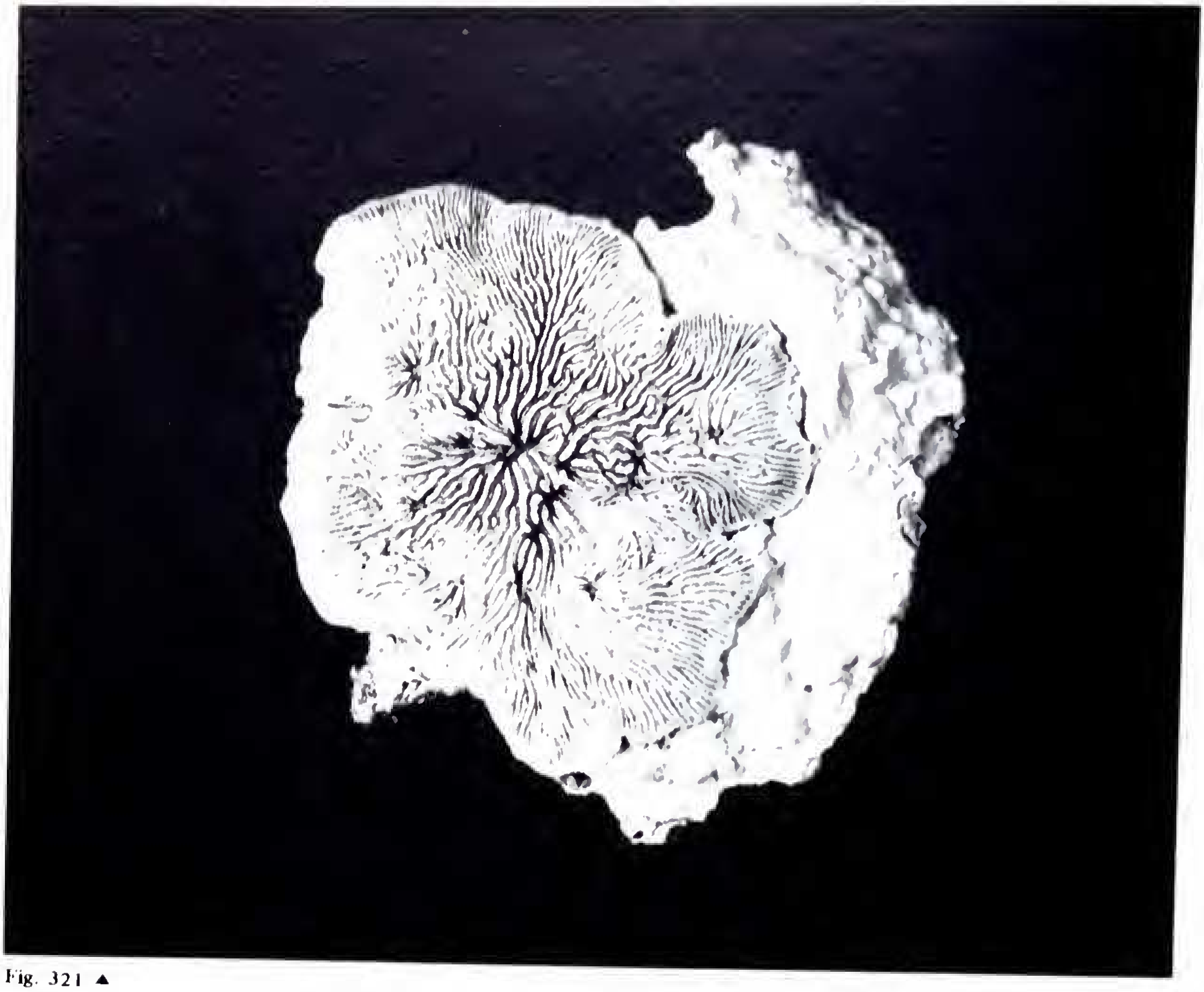
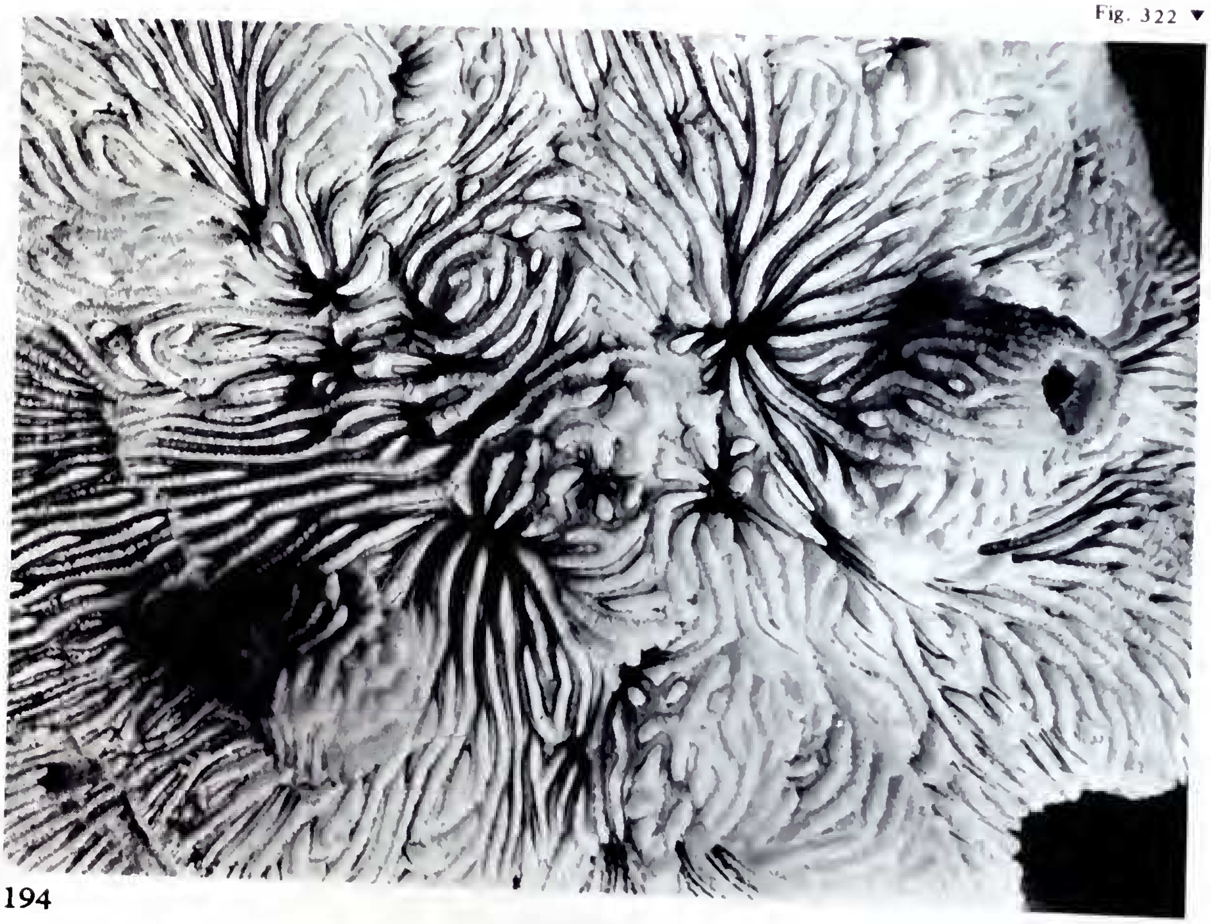


Fig. 321 ▲

Fig. 322 ▼



rounded lobes projecting upwards and a septo-costal ornamentation similar to that of *Cycloseris*. The homology between septo-costal structures strongly indicates that *Lithophyllon* is a polystomodeal derivative of *Cycloseris*.

Lithophyllon cf. edwardsi (Rousseau, 1854)

Synonymy

Leptoseris edwardsi Rousseau, 1854; Edwards & Haime (1860).

Lithophyllon undulatum Rehberg, 1892.

Podabacia dispar Verrill, 1901.

Podabacia elegans van der Horst, 1921; Yabe, Sugiyama & Eguchi (1936).

Podabacia lobata van der Horst, 1921.

Lithophyllon lobata (van der Horst); Utinomi (1965).

Lithophyllon elegans (van der Horst); Utinomi (1971).

Material studied

Darnley Island, Yorke Island, Murray Islands, Lizard Island (2 specimens), **Palm Islands** (8 specimens).

These localities include collecting stations 30, 31, 32, 42, 45, 90, 100, 126.

Previous records from Eastern Australia

Not previously recorded.

Figs. 321-323 *Lithophyllon* cf. *edwardsi*.

Fig. 321 From Lizard Island, collecting station 32 (× 1.0).
Fig. 322 From Esk Island, Palm Islands, collecting station 42 (× 2.5).
Fig. 323 From Pelorus Island, collecting station 90(× 5.0).

Fig. 323 ▼

Characters

Coralla are attached, unifacial, initially encrusting (up to about 8 cm diameter), then becoming foliaceous or laminar, with margins either regular and entire, or lobate and folded. They are about 10 mm thick at the centre, 2 mm at the periphery. They seldom exceed 10 cm maximum diameter. The central corallite remains visible in most coralla with secondary corallites becoming smaller towards the corallum periphery. Septa are arranged in a clearly radiating pattern from the corallum centre (Fig. 322), tending to become parallel at the margins. They are usually short (as little as 2 mm) in the central part of the colony, where principal septa are conspicuously higher and thicker than the others. They become longer and thinner towards the periphery and in the lobate parts of the corrallum but remain clearly alternate. New orders of septa regularly appear near the perimeter (Fig. 323). Septa abruptly decrease in height when they fuse laterally with two septa of the next highest cycle. In most coralla, the portion of septa situated just before the point of fusion is higher and thicker than the rest and thus resembles the tentacular lobes of solitary fungiids. It is not known whether this structure actually does correspond to the presence of tentacles in *Lithophyllon*. Septal margins are ornamented with numerous, small, very irregular granules, or appear laciniate and composed of irregularly contorted spiny processes. The upper part of septal sides may be perforate, the lower part is covered with granules. Upper margins of secondary septa are irregularly granular. Septal ornamentation therefore appears very similar to that of *Cycloseris*, particularly the *erosa/laciniosa* group of species. Columellae are spongiose or papillose and are well developed in the central part of the corallum, particularly in the central corallite. Synapticulae are visible on the oral side, at least in the peripheral part of the corallum.

The undersurface is imperforate. The free portions are covered with numerous thin, low, rounded costae, sometimes hardly visible to the naked eye. Their ornamentation is generally reduced to small smooth cones, or low bosses.

Lithophyllon cf. *edwardsi* is found mostly on the deeper outer reef slope and on middle and lower lagoon slopes.

Affinities

Van der Horst's specimens of *Podabacia dispar*, *P. lobata* and *P. elegans* appear to constitute only one species of *Lithophyllon*. The numerous forms of *Podabacia elegans* identified by Yabe *et al.* (1936) appear to be the same species. However, as noted by Wells (1966), the *Mycedium elegans* of Edwards & Haime is a *Leptoseris*, not a *Podabacia*, and of the existing names, *edwardsi* has priority. All specimens from Japan are large colonies, with large, frondose, curled lobes often projecting upwards. Principal septa towards the corallum periphery are very long, thin and laminar, with either ragged or entire margins. The central part has thickened, short, very alternating septa (Plate 49, Figs. 1 & 2 of Yabe *et al.*, 1936), and is in every respect similar to east Australian specimens which, for an unknown reason, do not develop beyond the encrusting to sublamellar stage. *Lithophyllon* cf. *edwardsi* collected recently in the Philippines and at Eniwetak Atoll have the same average size and the same encrusting growth form.

Of the two other described species of *Lithophyllon* (*L. levistei* Nemenzo, 1971 and *Podabacia formosa* Yabe, Sugiyama & Eguchi, 1936), the former is synonymous with *L.* cf. *edwardsi*, while the latter could be a distinct species. It is not possible, however, to decide this from the description and figures.

Distribution

Recorded from Indonesia, the Philippines, Japan, the Great Barrier Reef and Tonga.

Generic synonymy

Madrepora (*pars*); Pallas (1766); Esper (1791).

Agaricia (pars); Schweigger (1820).

Pavonia (*pars*); Dana (1846).

Podabacia Edwards & Haime, 1849c.

Halomitra (pars); Duncan (1883, 1884, 1889); Studer (1901).

Type species *Podabacia crustacea* (Pallas, 1766).

Characters of the genus (after Wells, 1966)

Coralla are polycentric, explanate or foliaceous, remaining attached to the substratum in the adult stage. Septo-costal structures are those of *Fungia* (*Verrillofungia*) and *Sandalolitha*.

Podabacia crustacea (Pallas, 1766)

Synonymy

Madrepora crustacea Pallas, 1766.

Madrepora pileus Esper, 1788; *non* Linnaeus (1758, 1767); *non* Pallas (1766).

Agaricia explanata Schweigger, 1829.

Pavonia explanulata Dana, 1846.

Podabacia crustacea Edwards & Haime, 1851a; Edwards & Haime (1860); Verrill (1863); Ortmann (1888, 1889); Studer (1877, 1880); Gardiner (1905); Bedot (1907); van der Horst (1921, 1922a); Matthai (1924); Faustino (1927); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Crossland (1952); Nemenzo (1955); Stephenson & Wells (1955); Searle (1956); Scheer (1964b).

Halomitra crustacea (Pallas); Duncan (1883).

Halomitra (*Podabacia*) *crustacea* (Pallas); Duncan (1889); Studer (1901).

Podabacia involuta van der Horst, 1921.

Material studied

Bramble Cay (2 specimens), **Darnley Island** (3 specimens), **Big Mary Reef, Yorke Island** (2 specimens), **Warrior Reef** (2 specimens), **Murray Islands** (3 specimens), **Turtle Backed Island** (2 specimens), **Dungeness Reef, Jervis Reef, Thursday Island, Jewell Reef** (2 specimens), **Yonge Reef, Lizard Island** (9 specimens), **Three Isles** (2 specimens), **Hope Island, Low Isles** (2 specimens), **Palm Islands** (25 specimens), **Pandora Reef, Magnetic Island, Bait Reef, Parker Reef** (3 specimens), **Whitsunday Island** (9 specimens), **Bushy Island-Redbill Reef** (2 specimens).

These localities include collecting stations, 3, 7, 11, 12, 13, 28, 29, 31, 32, 35, 39, 41, 42, 43, 45, 54, 55, 56, 57, 58, 67, 68, 69, 79, 80, 81, 85, 90, 91, 97, 98, 99, 102, 111, 119, 120, 122, 127, 131, 138, 139.

Previous records from Eastern Australia

Low Isles, Crossland (1952).

Characters and skeletal variation

Coralla are attached, unifacial, explanate, foliaceous or cup-shaped, with folded, lobate or curled margins (Fig. 758). They may be 1.5 m across and up to 15 mm thick at the centre. The central corallite is indistinct except in some cup-shaped specimens;

secondary centres are numerous and irregularly distributed except towards the corallum centre where concentric rows are usually discernible.

Septa are short, parallel and run perpendicular to the corallum periphery. Their extremities bend towards secondary centres, around which they radiate. Septa close to secondary centres are often petaloid in shape. Septa are strongly alternate in height and often in thickness. Principal septa are dentate with dentations up to 1.5 mm in height giving some coralla a rough appearance (Fig. 325); others are relatively smooth with more numerous dentations. There are 3-10 dentations between adjacent centres. Septa are thicker at their ends and corresponding dentations are higher and sometimes slightly thicker than the others. Septa usually increase in length and have increasingly smaller, more numerous dentations from the corallum centre to the periphery. Columellae may be absent, small or spongiose, but are never conspicuous. Synapticulae are numerous and clearly visible between adjacent septa (Fig. 327), except when these are very close to each other.

The undersurface is perforate with perforations sometimes reduced to inconspicuous, slit-like pores between costae. Costae are low and numerous and slightly alternate in size over the whole undersurface. They are covered with numerous *Fungia* (*Verrillofungia*)-like spines, with blunt tips and bearing small rounded granules. These vary greatly in size and may be almost invisible to the naked eye.

Affinities

Podabacia crustacea is a well defined species although not well represented in museum collections. Less dentate coralla of smaller specimens can resemble *Lithophyllon* and thus Yabe *et al.* (1936) included *L. elegans* in *Podabacia*.

Podabacia involuta van der Horst, 1921 is almost identical to less dentate coralla of the present series, although it is slightly more calcified.

Distribution

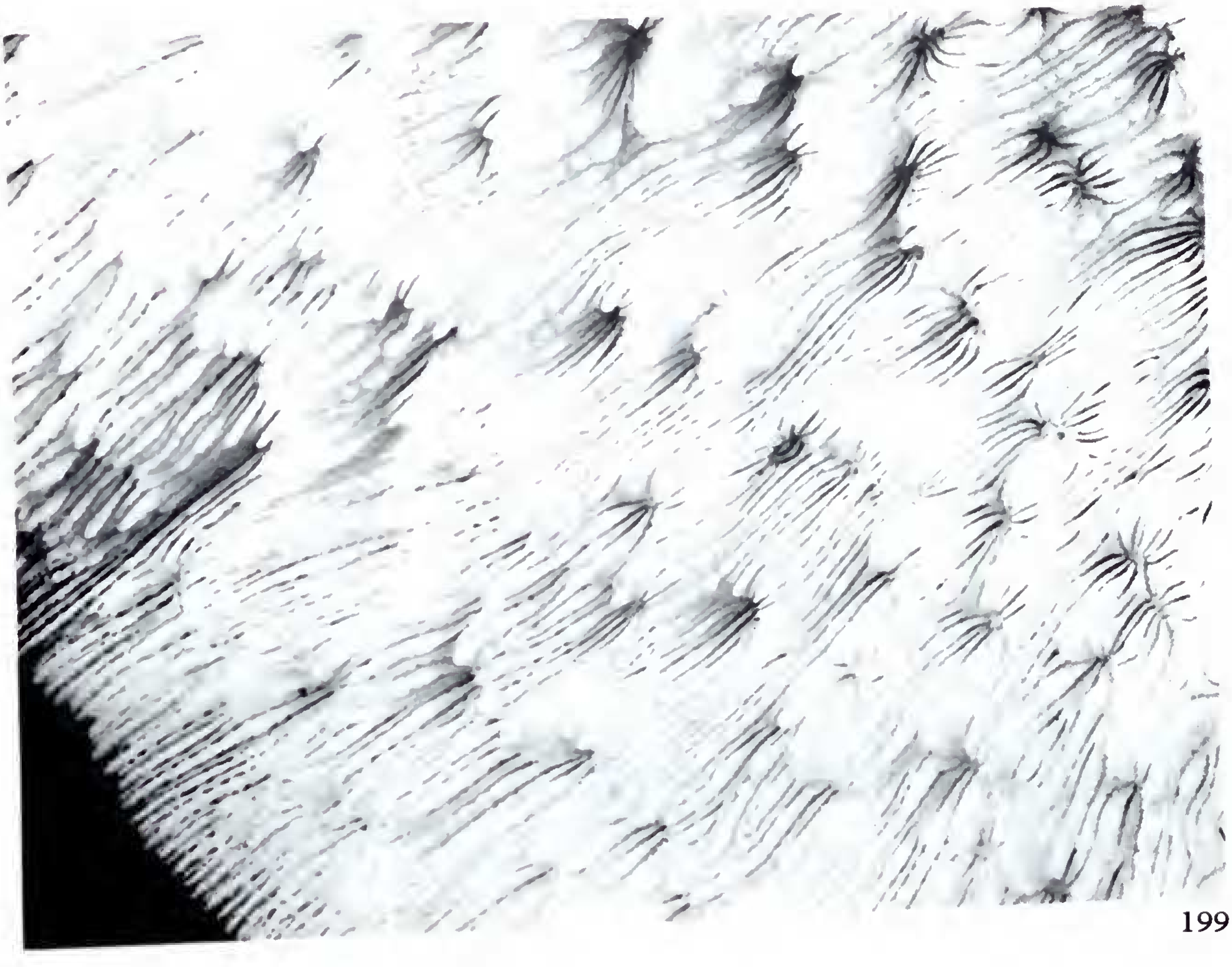
Widespread throughout the tropical Indo-Pacific from the Red Sea and Madagascar to Japan, the Marshall Islands and the Tuamotu Archipelago.

Figs. 324-327 *Podabacia crustacea*, Figs. 325-327 (× 2.5).

Figs. 324, 325 From the Swain Reefs, collecting station 69, Fig. 324 (× 1.0).
Fig. 326 From Bushy Island-Redbill Reef, collecting station 80.
Fig. 327 From Jewell Reef.

Fig. 324 ▲

Fig. 325 ▼



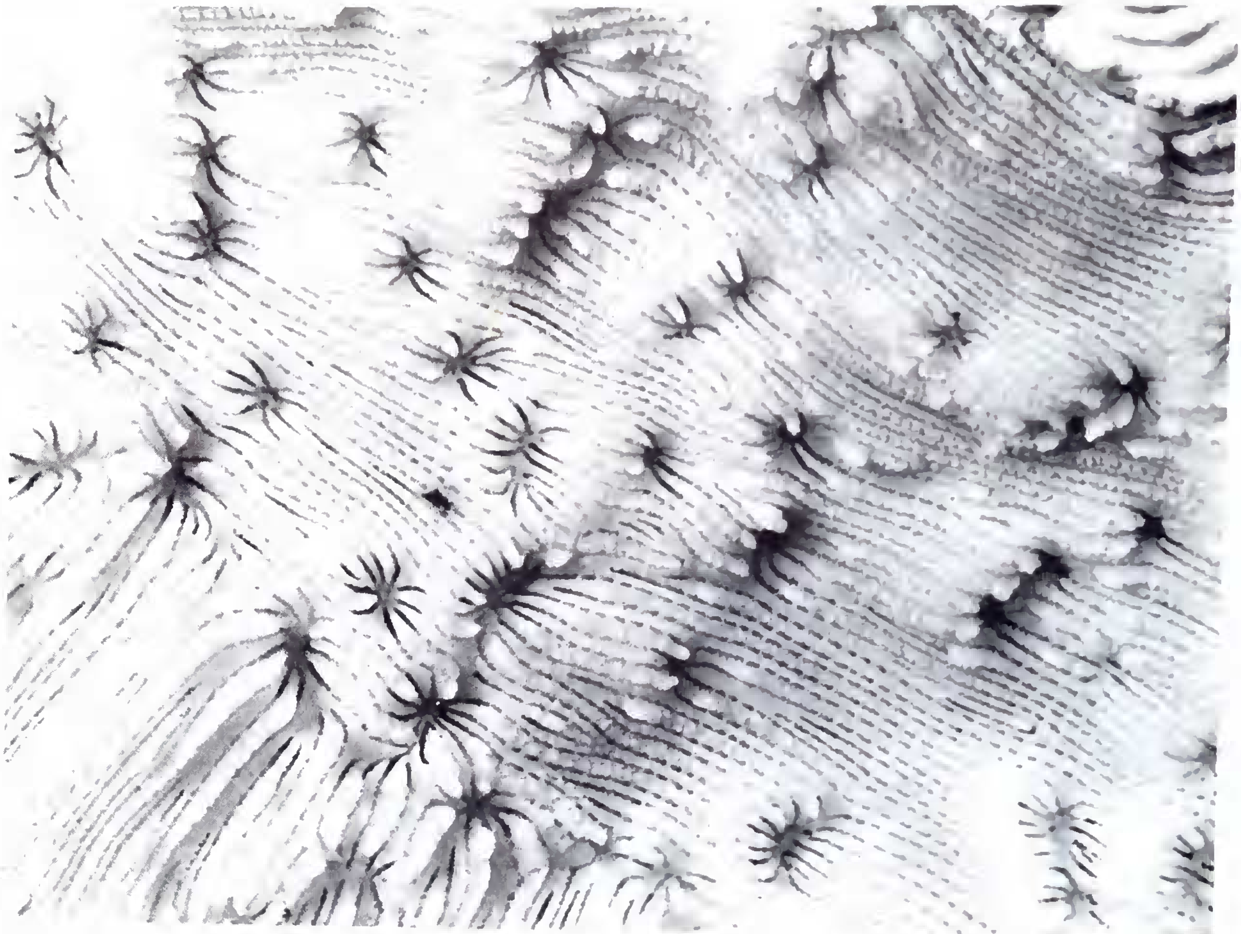


Fig. 326 ▲

Fig. 327 ▼

VI
Family Oculinidae Gray, 1847

Vaughan & Wells (1943) divided the Oculinidae into two subfamilies, the hermatypic Galaxeinae Vaughan & Wells, 1943 and the primarily ahermatypic Oculininae Gray, 1847. All east Australian hermatypic species belong to the Galaxeinae which has three recent genera, *Galaxea, Acrhelia* and *Simplastrea*. *Simplastrea* Umbgrove, 1939 is known from a single specimen only, which has a very doubtful taxonomic position. *Acrhelia* Edwards & Haime 1849b is monospecific while *Galaxea* Oken, 1815 contains 24 nominal species most of which have been dropped in earlier synonymies.

GENUS *GALAXEA* OKEN, 1815

Generic synonymy

Galaxea Oken, 1815; Edwards & Haime (1857); Matthai (1914); Chevalier (1971).

Type species *Madrepora fascicularis* Linnaeus, 1767.

Characters of the genus (after Wells, 1956)

'Massive, plocoid colonies formed by budding from broad edge zone of coenosarc. Corallites costate, cornute to cylindrical, united basally by extensive, vesicular, spinose, noncostate coenosteum. Columella absent or weak. Endothecal dissepiments weak and thin.'

Galaxea cf. astreata (Lamarck, 1816)

Synonymy

?*Madrepora musicalis* Linnaeus, 1767.

Caryophyllia astreata Lamarck, 1816.

Anthophyllum musicale (Linnaeus); Dana, 1846.

Anthophyllum clavus Dana, 1846.

Galaxea musicalis (Linnaeus); Edwards & Haime (1857); Matthai (1914); Thiel (1932); Yabe, Sugiyama & Eguchi (1936).

Galaxea clavus Dana, 1846; Edwards & Haime (1857); Vaughan (1918); Faustino (1927); Crossland (1952); Chevalier (1971).

Galaxea astreata (Lamarck); Chevalier (1971).

Vaughan (1918) has pointed out that the name *G. musicalis* is uncertain and should be dispensed. Most subsequent authors have followed this view and used the name *G. clavus* for this species. Chevalier (1971) revived the name of *G. astreata* and separated this species from *G. clavus* which he maintained separately but with doubts. The criteria for separating these species cannot be maintained in the present series and the older name, *G. astreata*, is consequently adopted.

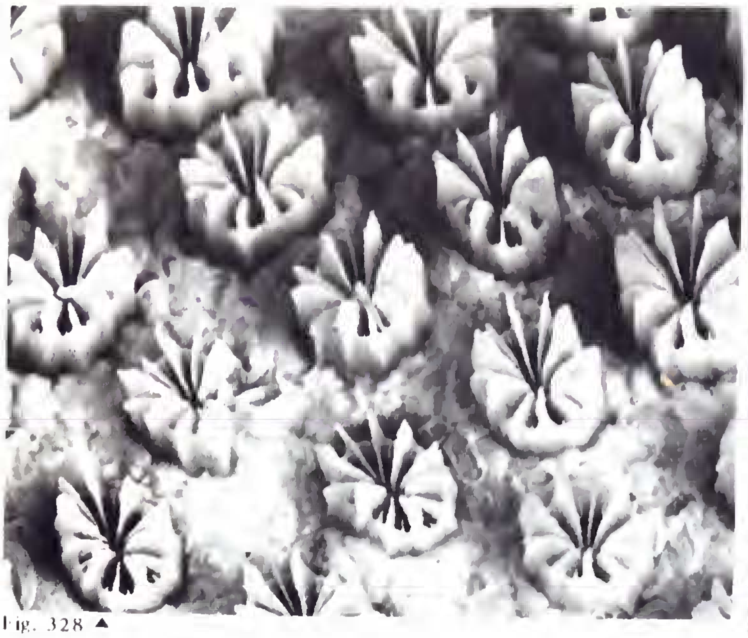


Fig. 328 ▲

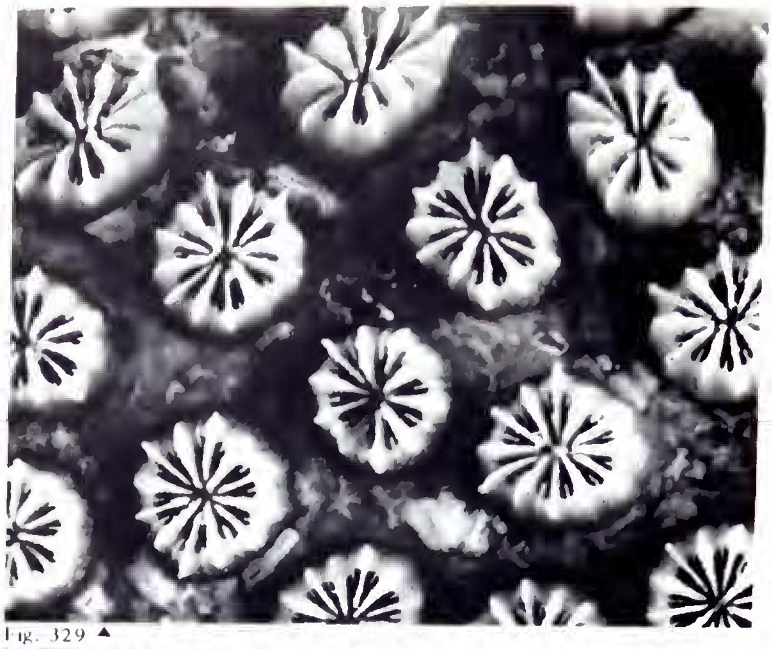


Fig. 329 ▲

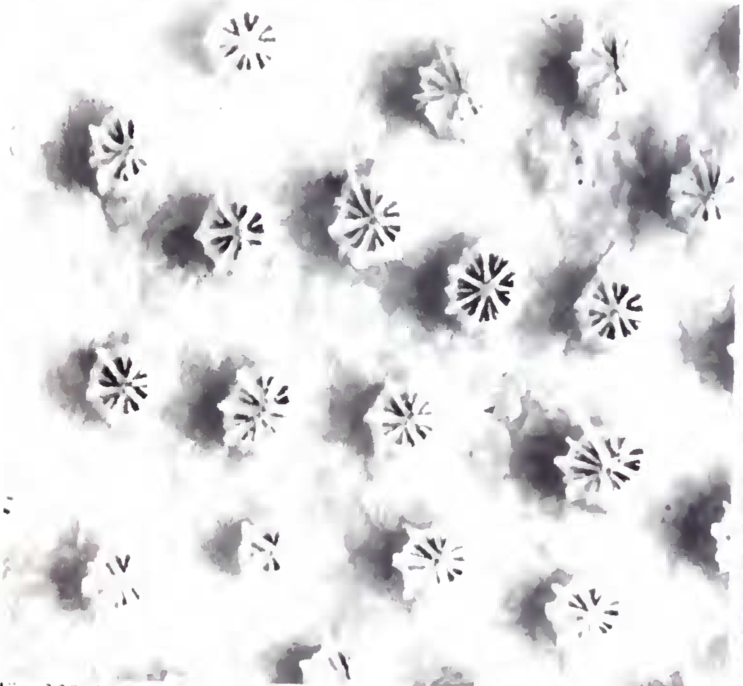


Fig. 330 ▲

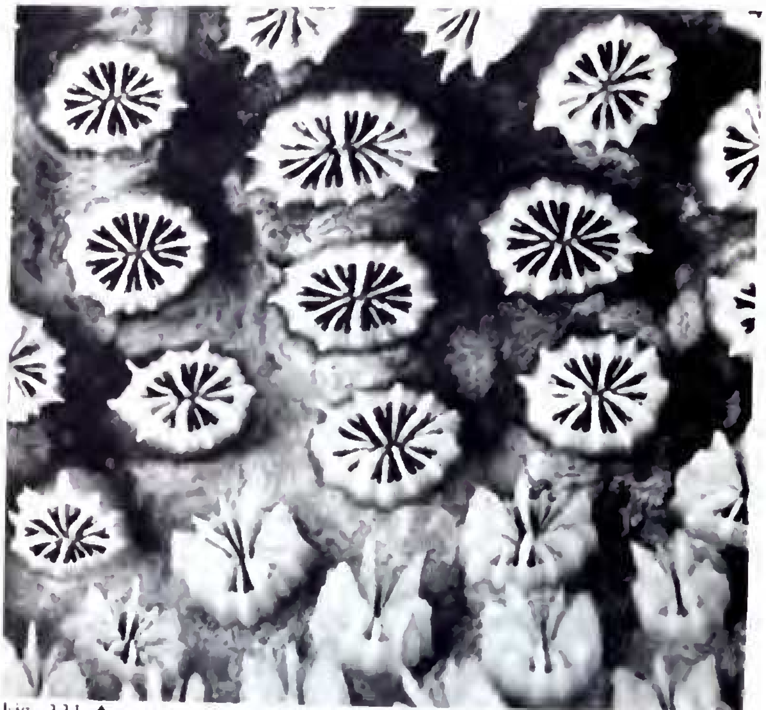
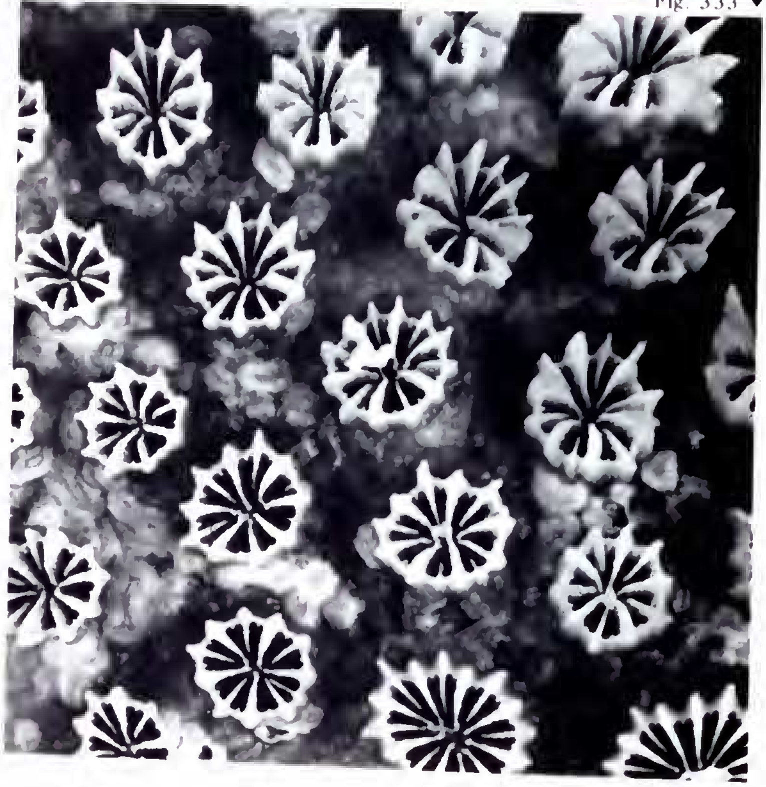


Fig. 331 ▲

Fig. 332 ▼

Fig. 333 ▼



Material studied

Warrior Island, Murray Islands (2 specimens), **Turtle Back Island, Lizard Island, Palm Islands** (4 specimens), **Plug Reef, Pandora Reef, Magnetic Island, Whitsunday Islands** (2 specimens), **Wistari Reef** (3 specimens), **Swain Reefs, Frigate Cay.**

These localities include collecting stations 28, 34, 36, 37, 38, 57, 60, 64, 69, 81, 97, 98, 111, 117, 118, 121, 138, 139.

Previous records from Eastern Australia

Cape York, Quelch (1886); **Low Isles,** Crossland (1952), Stephenson & Wells (1955); **Heron Island** (as *G. musicalis* and *G. clavus*) Salter (1954).

Characters

Colonies are usually small (<1 m diameter), encrusting, laminar, columnar or massive (Fig. 759). Mature corallites are circular or slightly elliptical and mostly uniform in size and appearance. They range from 3-4.5 mm diameter, are up to 3 mm exsert and are 2-3.5 mm apart. Septa are in 3 distinct cycles, the first two being subequal and up to 2 mm exsert. The third cycle is much smaller and usually projects inward less than half the calice radius. It may be absent in some coralla from deep water. Costae are usually subequal and inconspicuous. The inner margins of first and second cycle septa are usually in close proximity and may be thickened to form an incomplete pseudo-synapticular ring. The columellae, if present, are small and composed of a few septal dentations. The upper margins of the septa are smooth, their sides slightly granulated. The exotheca is finely blistered.

Living colonies are usually uniform in colour, usually pink or brown. Polyps are seldom expanded during the day (Fig. 760). Tentacles are usually translucent but may have white tips.

Figs. 328-333 *Galaxea* cf. *astreata* (× 0.5).

Figs. 328, 329 From Wistari Reef, collecting station 117.
Fig. 330 From the Palm Islands.
Fig. 331 From a plug reef south of Ribbon Reef, collecting station 64.
Fig. 332 From Frigate Cay, Swain Reefs, collecting station 81.
Fig. 333 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.

Fig. 334 *Galaxea* cf. *astreata* from the Swain Reefs, with polyps retracted during the day.

Fig. 334 ▼

Affinities

This species is readily distinguished from *G. fascicularis* by having smaller, more uniform corallites with only three cycles of septa.

Distribution

Previous records are from the Red Sea, Indian Ocean, Indonesia, New Caledonia and Fiji. The species appears to be absent from most western Pacific reefs.

Galaxea fascicularis (Linnaeus, 1767)

Synonymy (partly after Matthai, 1914 and Chevalier, 1971)

Madrepora fascicularis Linnaeus, 1767.

Galaxea fascicularis (Linnaeus); Edwards & Haime (1857); Brüggemann (1879a); Klunzinger (1879); Quelch (1886); Ortmann (1888, 1892); Gardiner (1899a, 1904); Bedot (1907); Gravier (1911); Matthai (1914); Vaughan (1918); Hoffmeister (1925); Faustino (1927); Thiel (1932); Crossland (1935, 1938, 1941, 1952); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1940); Rossi (1954); Stephenson & Wells (1955); Boschma (1959); Nemenzo (1959); Scheer (1967); Ma (1959); Chevalier (1971); Scheer & Pillai (1974).

? *Galaxea esperi* (Schweigger, 1820).

Galaxea ellisi (Edwards & Haime); Edwards & Haime (1857); Quelch (1886); Ortmann (1888, 1892); Gravier (1911).

Galaxea irregularis (Edwards & Haime); Edwards & Haime (1857); Klunzinger (1879); Ortmann (1888); von Marenzeller (1907).

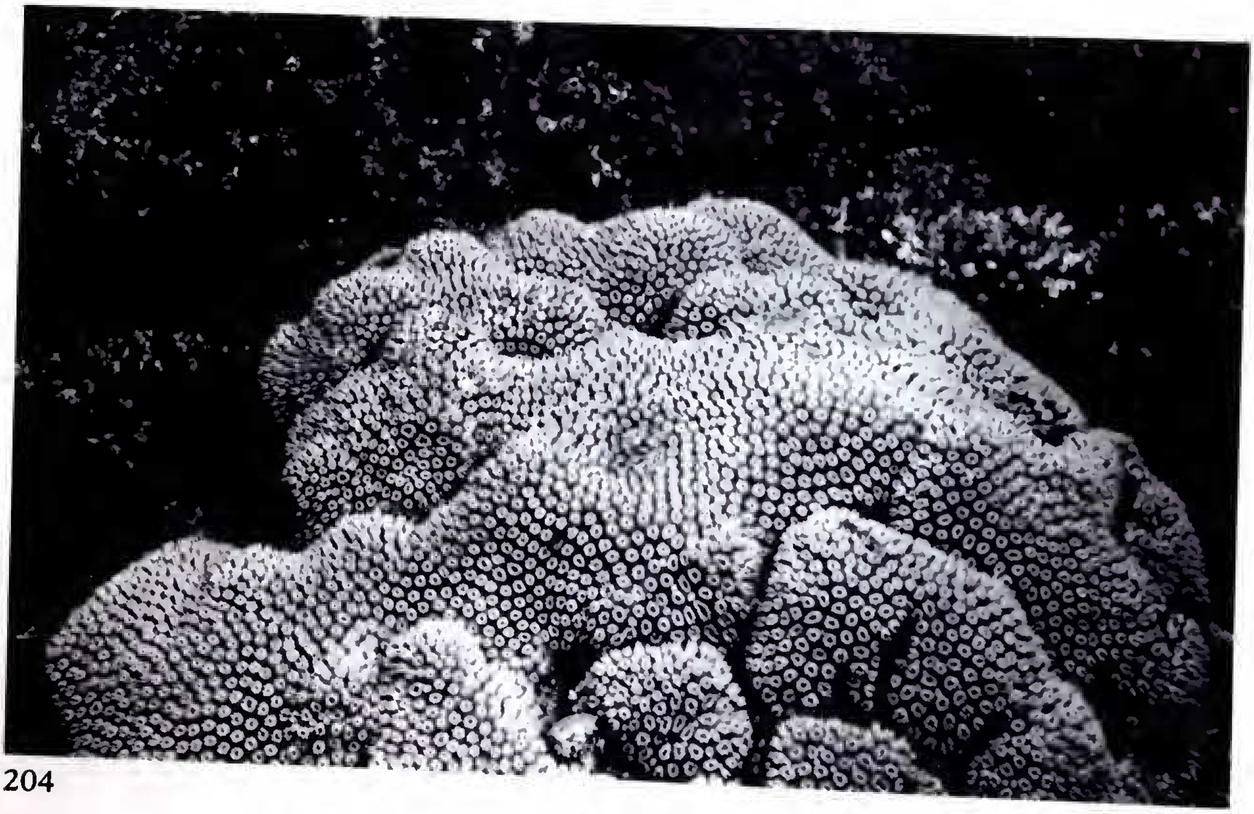
Galaxea quoyi (Edwards & Haime); Edwards & Haime (1857).

Galaxea aspera Quelch, 1886; Bernard (1900); Bedot (1907); Faustino (1927).

Galaxea heterocyathus Ortmann, 1889.

Galaxea hystrix Dana, 1846.

Fig. 335 *Galaxea* cf. *astreata* from the Swain Reefs.



? *Galaxea hexagonalis* (Edwards & Haime); Edwards & Haime (1851c, 1860); Gardiner (1904); Matthai (1914, 1923a); Faustino (1927).

? *Galaxea fragilis* Quelch, 1886.

Galaxea tenella Brüggemann, 1879b; Quelch (1886).

Galaxea lawisiana Nemenzo, 1959.

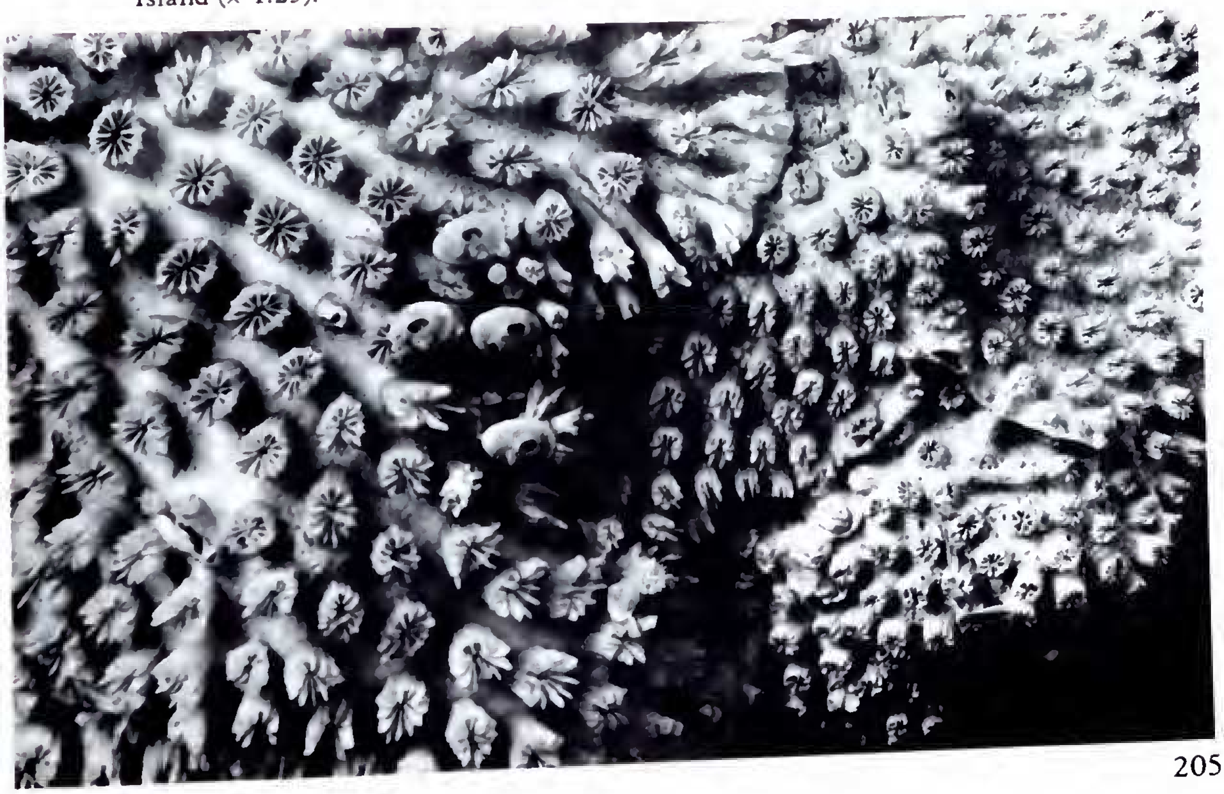
This synonymy, which is far from complete, reflects the wide range of skeletal variation of *G. fascicularis*. Six species were originally synonymised by Edwards & Haime (1857) and Matthai (1914) largely completed and updated this list which is now of historical interest only. Chevalier (1971) divided *G. fascicularis* into eight named varieties and gave notes on ten nominal species which are compared with each other and with his varieties.

Material studied

Barrier Reef NE of Murray Island (2 specimens), **Yorke Island, Murray Island, Sue Islet, Big Mary Reef** (3 specimens), **Jervis Reef, Wai Weer Island** (3 specimens), **Great Detached Reef** (2 specimens), **Tijou Reef, Bewick Island, Jewell Reef, Waining Reef** (2 specimens), **Lizard Island, MacGillivray Island, Hope Island, Low Island** (5 specimens), **Palm Islands** (62 specimens), **Pandora Reef** (4 specimens), **Gould Reef** (2 specimens), **Parker Reef, Whitsunday Islands** (5 specimens), **Pompey Complex, Frigate Cay** (2 specimens), **Heron Island** (3 specimens), **Wistari Reef** (3 specimens).

These localities include collecting stations 1, 2, 5, 12, 13, 17, 27, 34, 35, 36, 38, 39, 41, 42, 43, 45, 55, 57, 59, 60, 61, 62, 72, 74, 81, 90, 97, 98, 99, 108, 111, 113, 116, 117, 118, 119, 125, 128, 131, 132, 135, 139.

Fig. 336 Adjacent coralla of *Galaxea fascicularis* (left) and *Galaxea* cf. *astreata* (right), from Lizard Island (× 1.25).



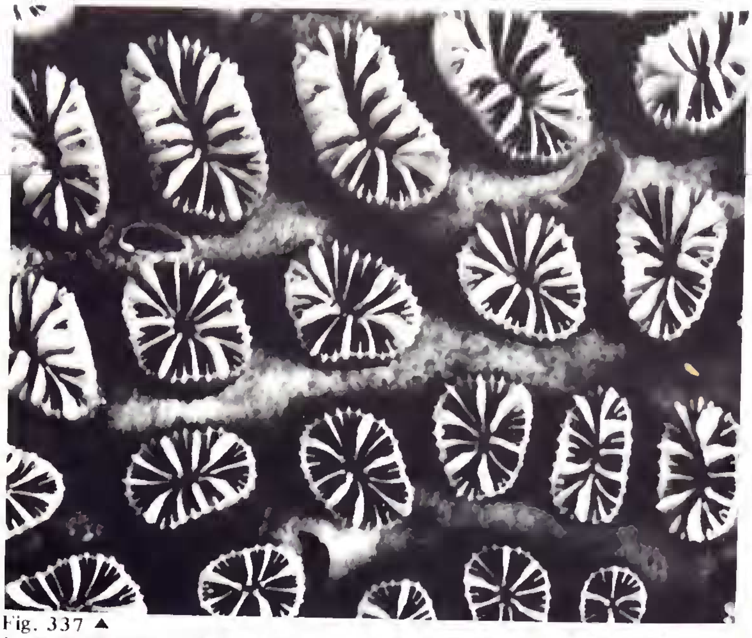


Fig. 337 ▲

Fig. 338 ▲

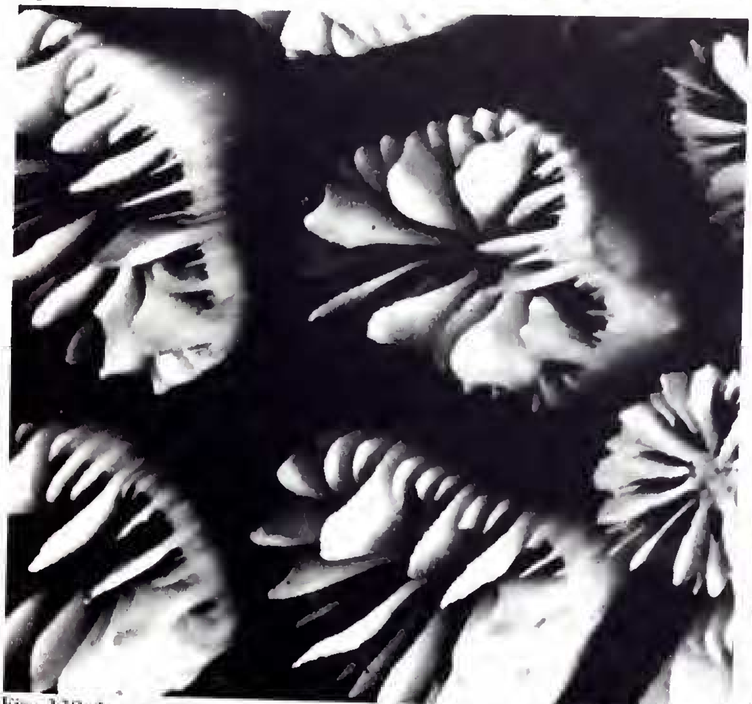


Fig. 339 ▲

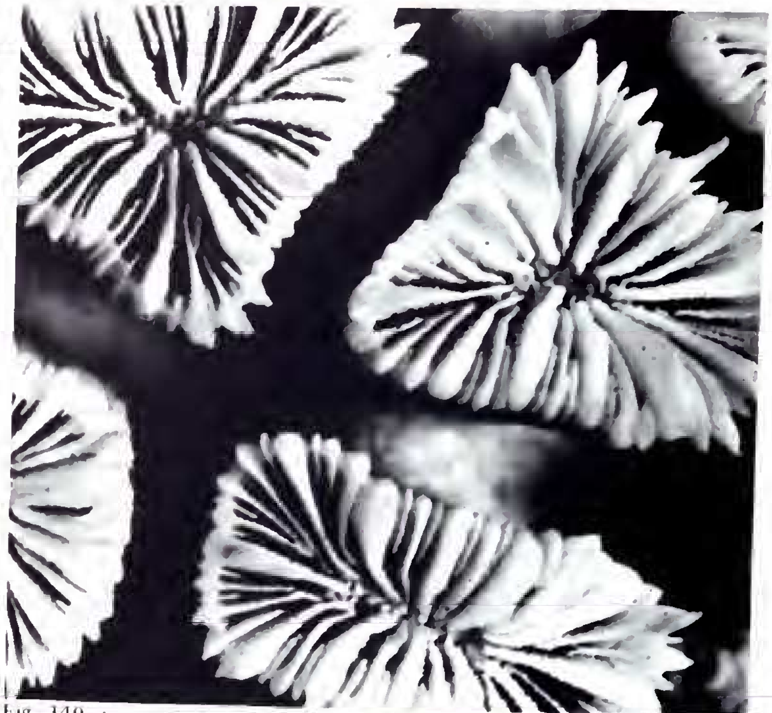


Fig. 340 ▲

Fig. 341 ▼

Fig. 342 ▼

Previous records from Eastern Australia

Murray Islands, Vaughan (1918); **Low Isles,** Yonge (1930, 1940), Yonge & Nicholls (1931a, 1931b), Marshall & Orr (1931), Yonge, Yonge & Nicholls (1932), Manton (1935), Crossland (1952), Stephenson & Wells (1955); **Heron Island,** Salter (1954).

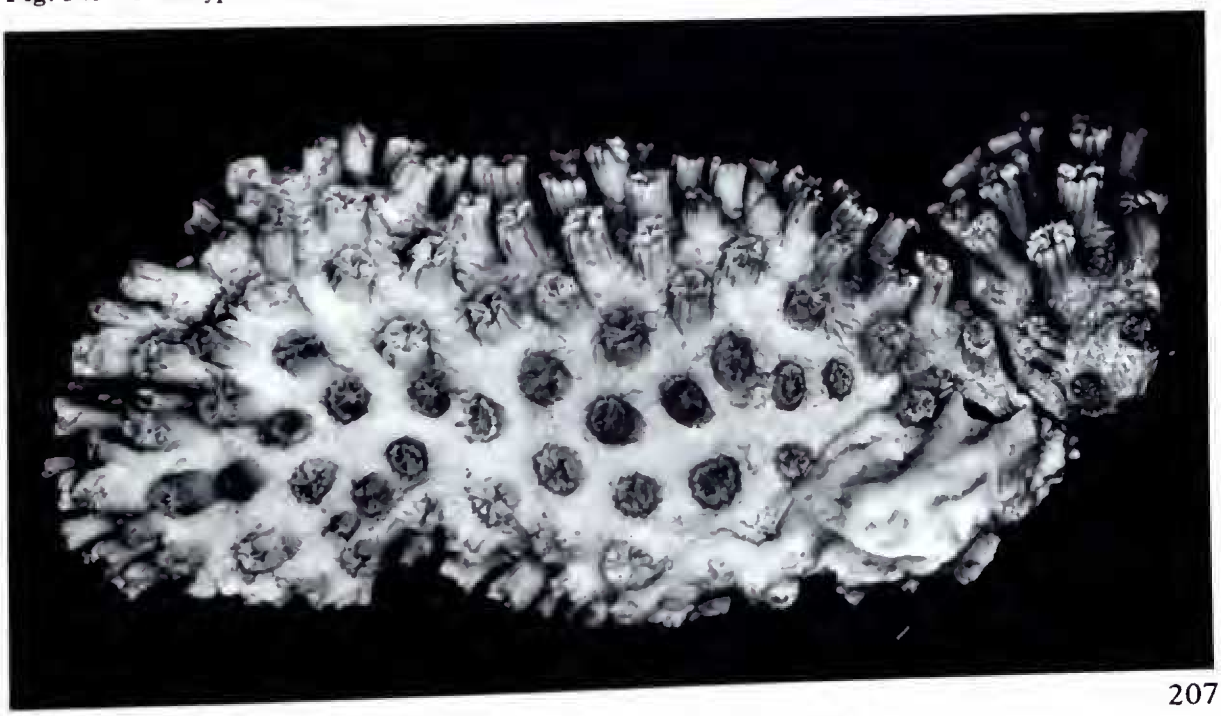
Characters

Small colonies usually take the form of low domes or 'cushions' or are sub-digitate (Fig. 762). Larger colonies may be flat, hemispherical, columnar or sub-digitate (Fig. 761), depending largely on environmental conditions. Columnar growth forms are common, with colonies frequently exceeding 2 m in height and 5 m in diameter. The columns, which are usually <10 cm diameter, are usually only loosely interconnected (Fig. 347). Corallites characteristically show an enormous range of variation, especially on coralla with irregular surfaces or those infested by boring organisms (Fig. 342). Corallites are usually irregular in shape, depending on how closely they are packed and on their position on the corallum Four cycles of septa are usually present although the fourth cycle may not develop in coralla from deep water and a fifth cycle may be partly formed in large calices. The first two cycles may be equal or very unequal. In most corallites they are very exsert; in many they are irregularly contorted. The costae are likewise very variable. Those of the first two cycles are usually subequal and prominent. In some coralla they may be almost equal to the septa in size. The columellae are weakly developed or absent. In some coralla the columellae are surrounded by a pseudo-synapticular ring made up of the inner margins of the first and second cycle septa. All septa and costae have granulated sides and may have granulated margins. The walls are primarily septothecate. The development of the exotheca varies greatly throughout the range of the species. In some coralla, individual corallites appear as long tapering tubes, interconnected by

Figs. 337-342 *Galaxea fascicularis*, Figs. 337-340.

Figs. 337, 339	From Fantome Island, Palm Islands, collecting station 34 (× 2.5 and 5.0) respectively.
Figs. 338, 340	From Wistari Reef, collecting station 117 (× 2.5 and 5.0) respectively.
Fig. 341	From Sue Island, collecting station 17 (× 2.5).
Fig. 342	From the Swain Reefs (× 5.0).

Fig. 343 Holotype of *Galaxea fascicularis.*



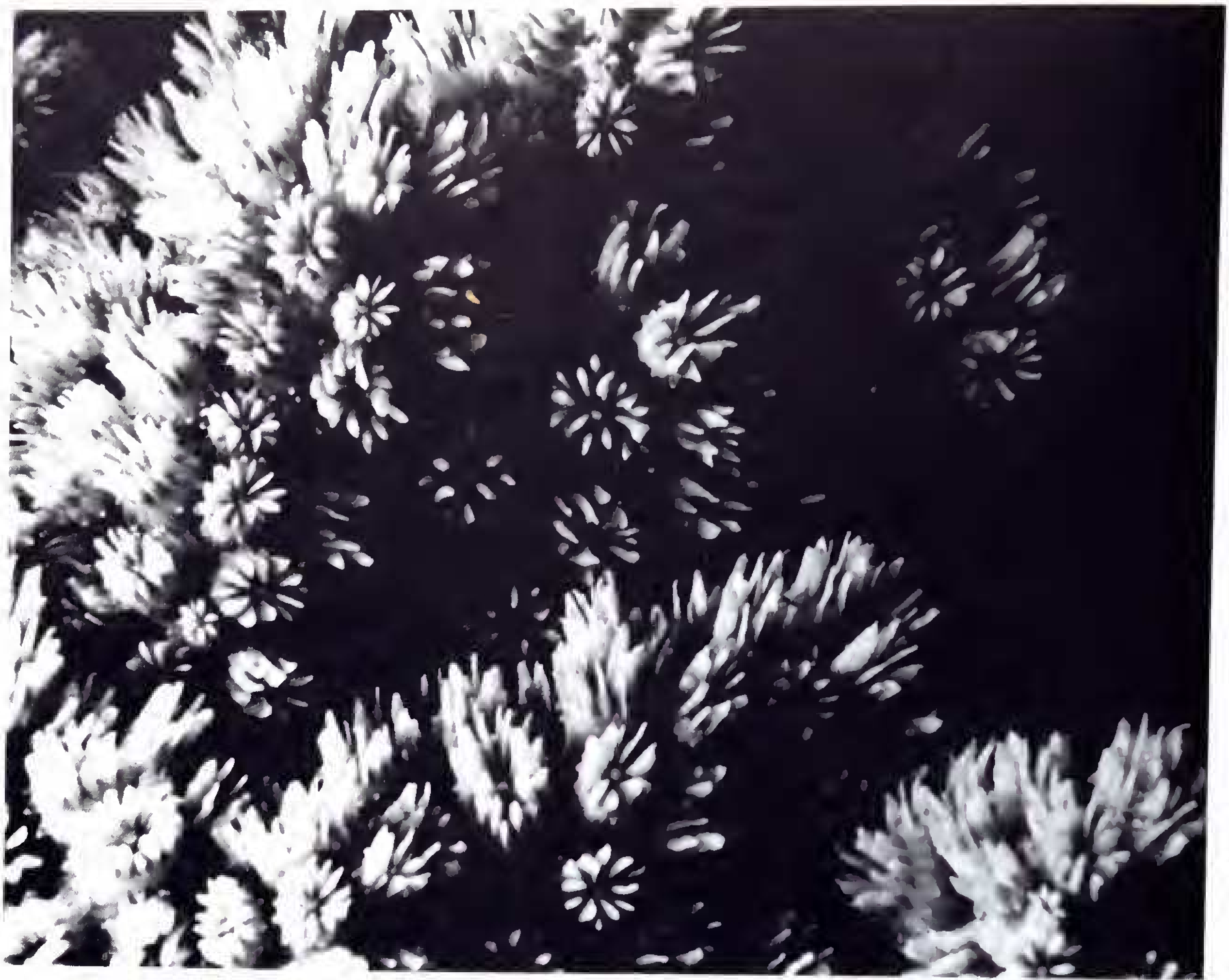
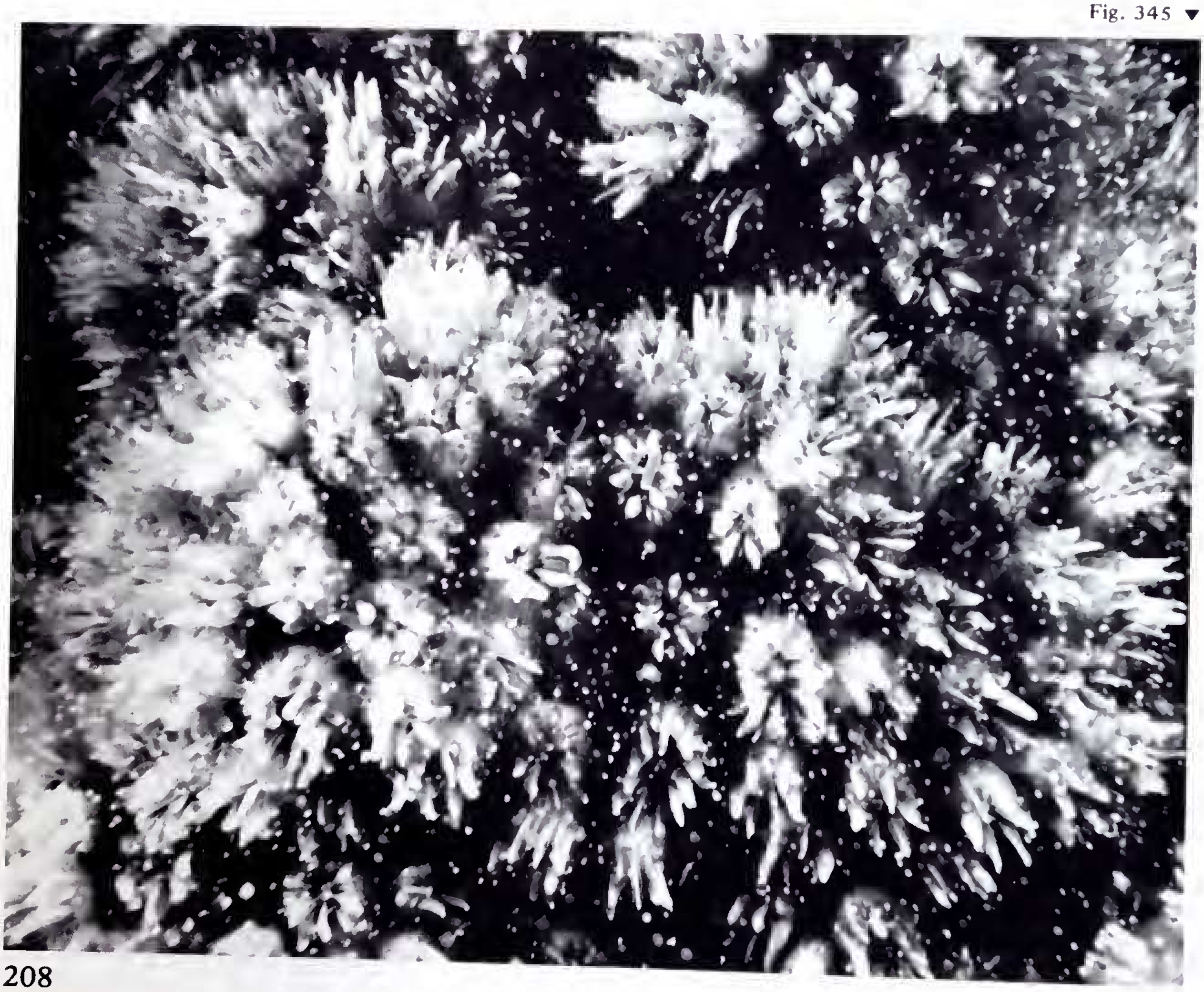


Fig. 344 ▲

Fig. 345 ▼



fine layers of exothecal dissepiments spaced at intervals of up to 1 cm. Budding is usually basal.

Polyps are frequently expanded during the day. Those from shallow water are usually colourful with greens, reds and browns predominating. Those from turbid water are usually grey or brown. Tentacles usually have conspicuous white tips (Fig. 345).

Skeletal variation

Galaxea fascicularis from shallow reef biotopes.

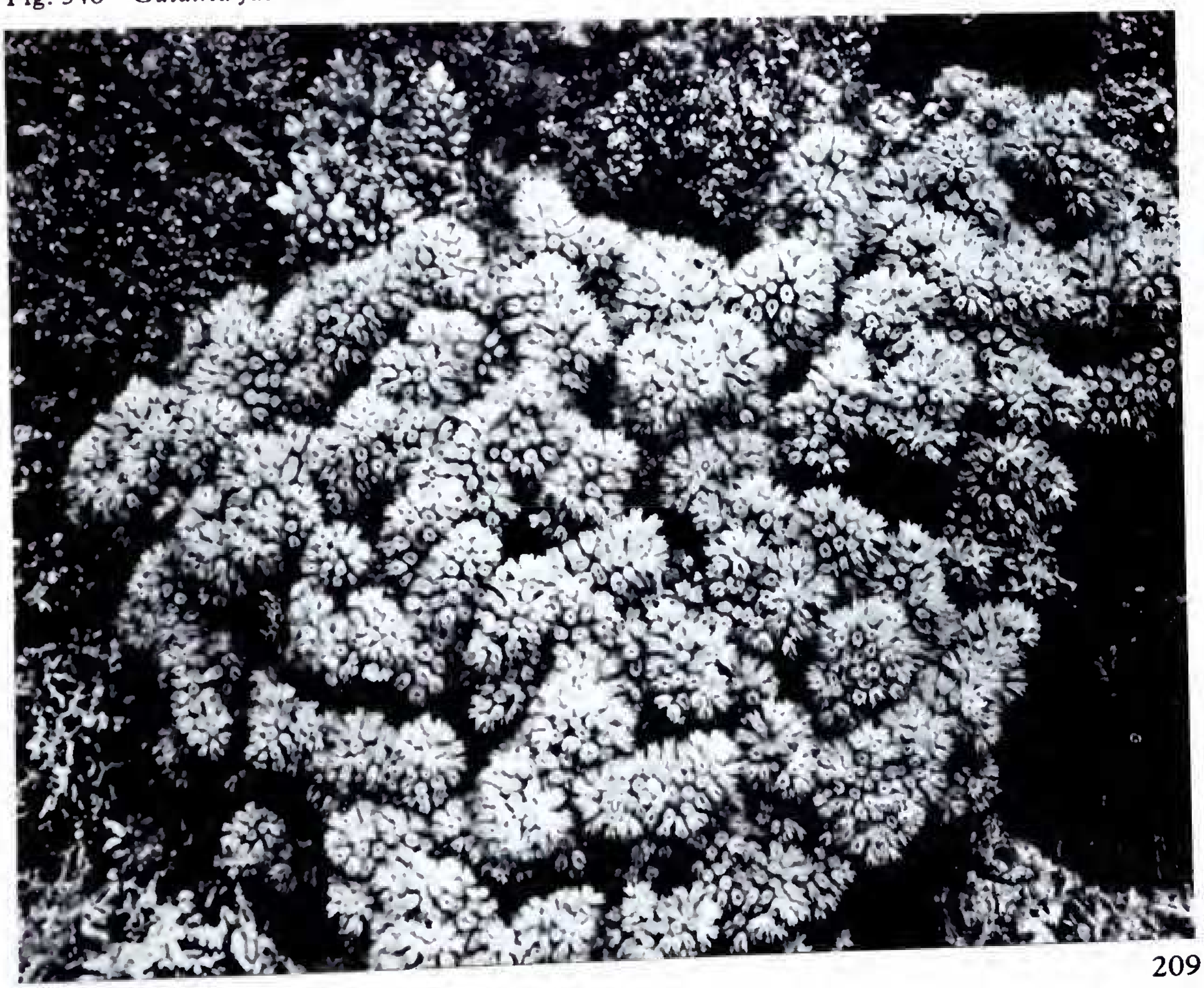
Coralla are usually dome shaped with an even, undulating surface. Those protected from wave action are frequently subdigitate.

Galaxea fascicularis from turbid biotopes.

The majority of large colonies of this species occur in conditions of reduced light intensity, especially in partly turbid water with tidal currents. Such colonies usually have columnar growth forms. Corallites of the same colony have a wide range of variation in size and appearance. Septa are almost always in four cycles, those of the first two cycles are usually very exsert and may be very irregular in shape.

Figs. 344, 345 *Galaxea fascicularis* from the Swain Reefs, showing the appearance of the polyps during the day (Fig. 344) and when extended at night (Fig. 345).

Fig. 346 *Galaxea fascicularis* from the Swain Reefs.



Galaxea fascicularis from deep water.

At the lower limit of its bathymetric range or in other conditions of very reduced light intensity, *G. fascicularis* usually has encrusting or laminar growth forms. Corallites are widely spaced and relatively small. Up to approximately 80 per cent of the corallum surface area is composed of finely blistered coenosteum. In many such coralla, only three septal cycles are developed. These have a very regular, hexameral appearance.

Coralla from deep water are frequently infested with barnacles and boring organisms which induce extremely irregular corallites.

Affinities

This species is readily distinguished from *G.* cf. *astreata* by its growth form, the size of the corallites and the number of septa (Fig. 336). The growth form is usually columnar, the corallites are usually large and the septa are usually in 4 cycles. Coralla from deep water come closest to reefal *G.* cf. *astreata* and may differ only in having more widely spaced corallites and a fine, blistered coenosteum.

Distribution

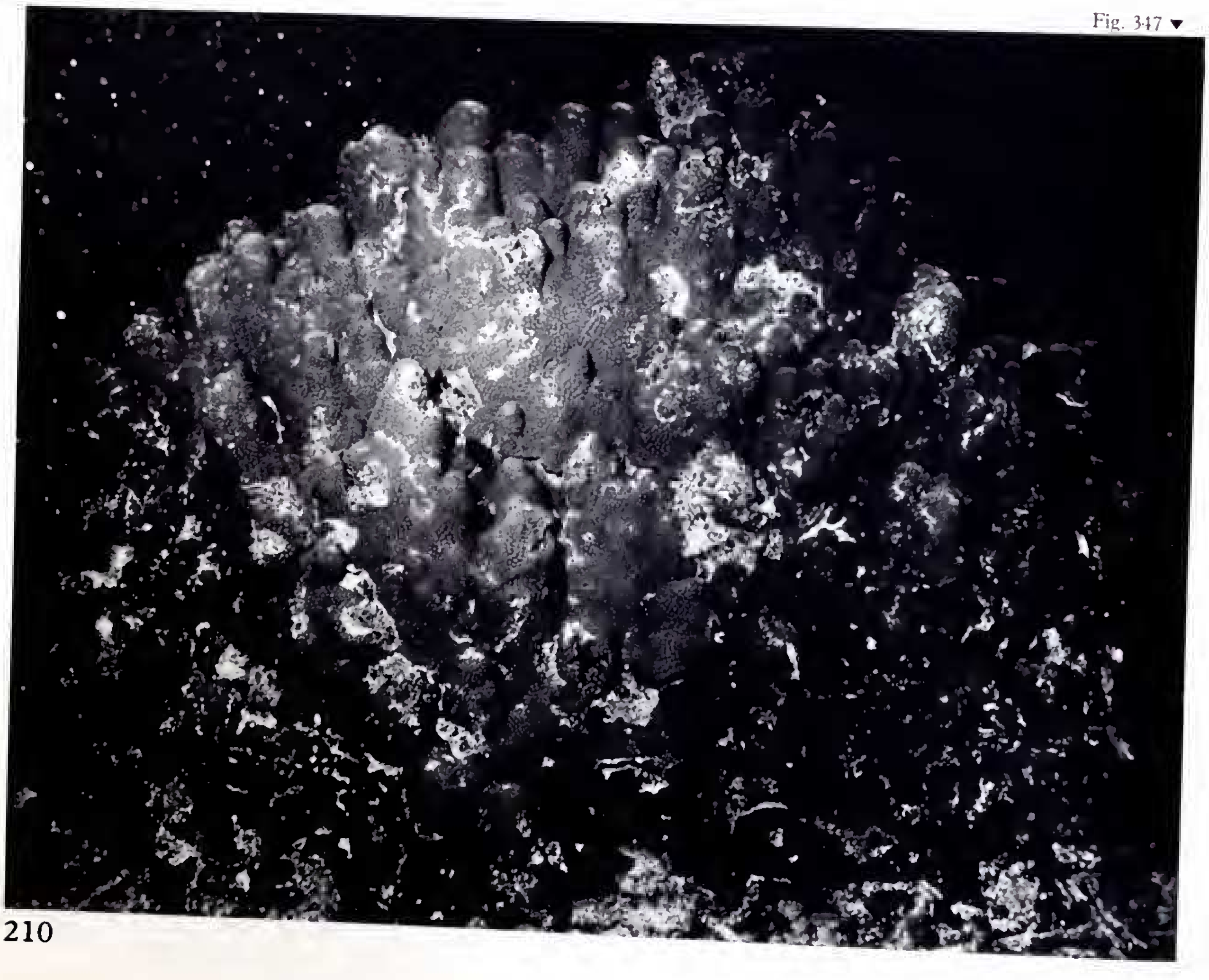
Widely distributed from the Red Sea to the tropical western Pacific including Fiji and Samoa.

Fig. 347 *Galaxea fascicularis* from Heron Island.

Figs. 348-350 *Acrhelia horrescens* (× 0.5).

Fig. 348 From the Pompey Complex.
Fig. 349 From Bowl Reef, collecting station 10.
Fig. 350 From the Pompey Complex, collecting station 75.

Fig. 347 ▼



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Generic synonymy

Acrhelia Edwards & Haime, 1849c; Vaughan & Wells (1943); Wells (1956).

Acrohelia (Edwards & Haime); Edwards & Haime (1857); Chevalier (1971).

Type species *Acrhelia sebae* Edwards & Haime = *Oculina horrescens* Dana, 1846.

Acrhelia is a monospecific genus distinguished from *Galaxea* by the formation of completely ramose colonies. Otherwise these genera are distinguished only on minor, specific characters.

Acrhelia horrescens (Dana, 1846)

Synonymy (the spellings *Acrhelia* and *Acrohelia* are not differentiated) *Oculina horrescens* Dana, 1846.

Acrhelia horrescens (Dana); Edwards & Haime (1857); Quelch (1886); Ortmann (1888); Vaughan (1918); Thiel (1932); Umbgrove (1940); Crossland (1952); Wells (1954); Nemenzo (1959); Chevalier (1971).

Material studied

Murray Islands, Bowl Reef (3 specimens), **Bushy Island-Redbill Reef, Parker Reef, Pompey Complex** (3 specimens), **Heron Island.**

These localities include collecting stations 10, 30, 72, 75, 80, 112, 115.

Previous records from Eastern Australia

Murray Islands, Vaughan (1918), Mayer (1918), Yonge (1930); **Heron Island,** Salter (1954).

Characters

Colonies may be small and irregular in shape or large (up to 2 m diameter) and hemispherical (Fig. 357). They are composed of masses of thin anastomosing branches which may be dense and bushy or open and widely separated (Figs. 348-350, 763), depending on environmental conditions. In either case, branches are mostly straight and relatively uniform in diameter (6-12 mm). The angle of branching averages approximately 60° in most colonies. Branches have terminal corallites or a cluster of branch-end corallites. Budding occurs mostly at the base of small terminal corallites and these tend to spiral around branches. Older corallites are asymmetrical in shape with their central axis curved outwards to be nearly perpendicular to the branch axis. Thecae protrude up to 35 mm from the branches and increase in diameter to approximately 2.5 mm at the rim.

Septa have a hexameral arrangement and are in three, rarely four, cycles. They are extremely exsert (up to 4 mm). All septa have smooth margins and finely granulated sides. Costal ridges are only weakly developed although the walls are primarily septothecate. Calices are very deep and there is no externally visible columella. The coenosteum is finely vesicular and usually minutely granulated.

Living colonies are usually pale brown or green with white branch ends. Expanded polyps have tapering translucent tentacles with white tips, similar to those of *G. fascicularis* (Fig. 364).

Figs. 351-354 *Acrhelia horrescens* (× 2.5).

Figs. 351, 353, 354 Showing calices from different parts of the same corallum from the Pompey Complex, same corallum as Fig. 350.

Fig. 352 From Bowl Reef, same corallum as Fig. 349.

Fig. 351 ▲

Fig. 352 ▲

Fig. 353 ▼

Fig. 354 ▼

Fig. 355 ▲

Figs. 355, 356 *Acrhelia horrescens* from the Swain Reefs showing the appearance of the polyps during the day (Fig. 355) and when extended at night (Fig. 356).

Fig. 356 ▼

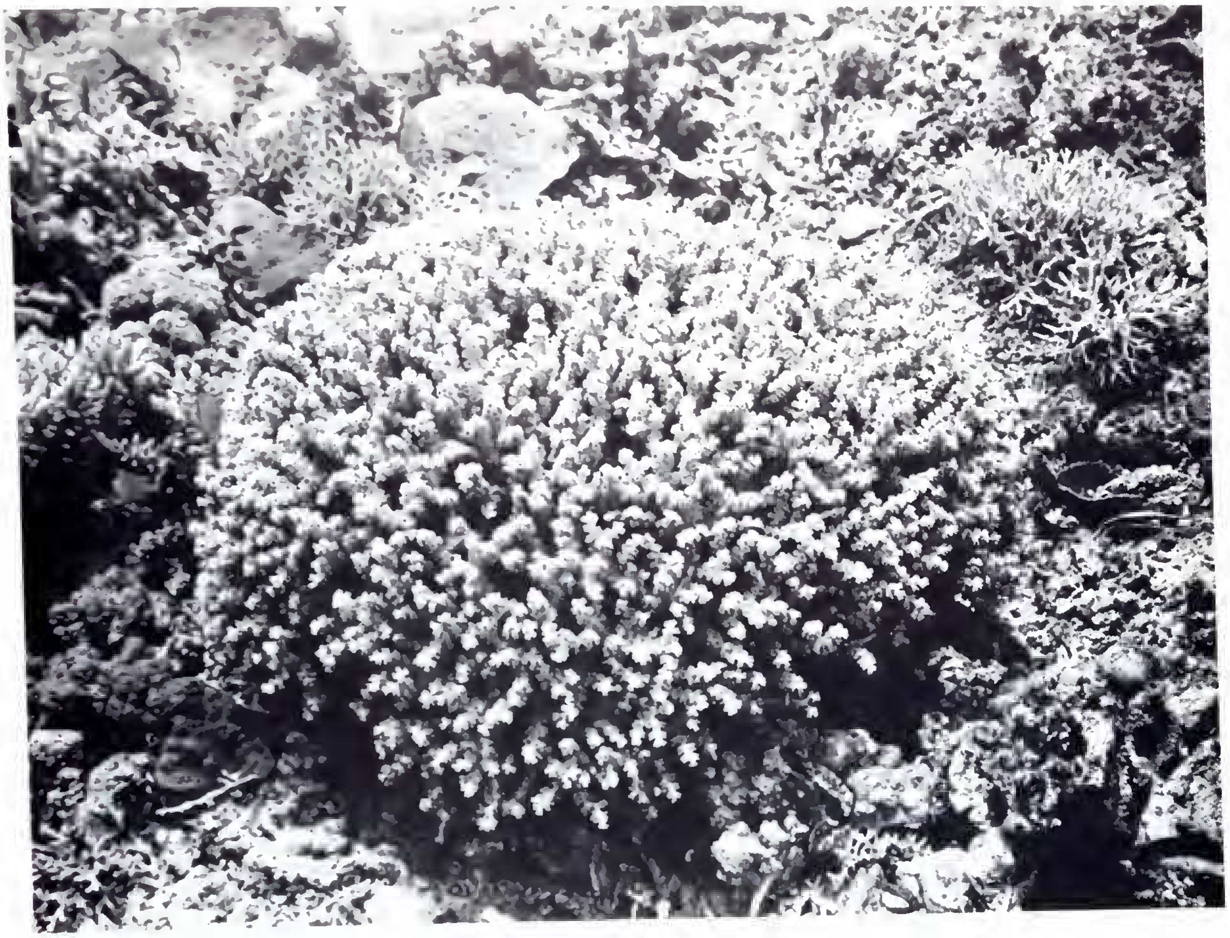


Fig. 357 *Acrhelia horrescens* from the Swain Reefs.

Growth form variation

This species is seldom abundant and is entirely restricted to reefal biotopes with good water circulation and light availability. With increasing depth branching becomes increasingly lax.

Distribution

Recorded from the tropical western Pacific including Indonesia, the Philippines, the Marshall Islands, New Hebrides and Fiji.

VII
Family Merulinidae Verrill, 1866

Three of the four genera of Merulinidae are found on the Great Barrier Reef, each represented by a single species. The fourth genus, *Boninastraea* Yabe & Sugiyama 1935, also represented by a single species, *B. boninensis* Yabe & Sugiyama 1935, is known only from the holotype. This specimen has a doubtful taxonomic position and is included in the Mussidae by Yabe & Sugiyama (1935) and Yabe *et al.* (1936) and in the Merulinidae by Wells (1956) and Ma (1959).

GENUS *MERULINA* EHRENBERG, 1834

Generic synonymy

Merulina Ehrenberg, 1834; Edwards & Haime (1857); Matthai (1928).

Type species *Madrepora ampliata* Ellis & Solander, 1786.

Introduction

The taxonomy of *Merulina* has previously been confused with that of *Hydnophora* and *Clavarina*. Thus, *Merulina laxa* Dana, 1846, *Merulina prolifera* Quelch, 1886 and *Clavarina composita* Rehberg, 1892 are all synonyms of *Merulina* (= *Hydnophora*) *rigida* Dana, 1846 (Veron *et al.*, 1977, p. 124). The remaining nominal species of *Merulina* all appear to be junior synonyms of *M. ampliata*, *Clavarina scabricula* or (as with *M. studeri* Bedot, 1907) *Scapophyllia cylindrica* and the genus consequently appears to be monospecific.

Merulina ampliata (Ellis & Solander, 1786)

Synonymy

Madrepora ampliata Ellis & Solander, 1786; Esper (1797).

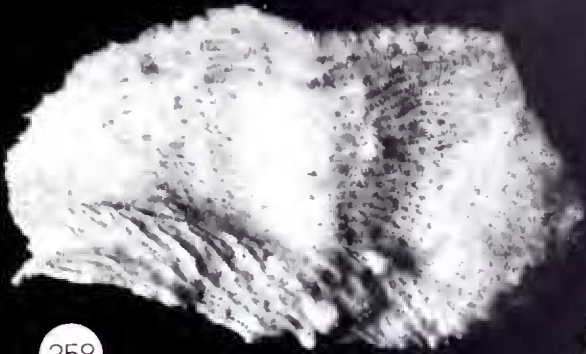
Agaricia ampliata (Ellis & Solander); Lamarck (1801); Fischer de Waldheim (1807).

Merulina ampliata (Ellis & Solander); Dana (1846); Edwards & Haime (1851a, 1857); Verrill (1864); Duncan (1884); Ortmann (1888, 1889); Studer (1880); Gardiner (1904); Bedot (1907); Vaughan (1918); van der Horst (1921); Matthai (1923a, 1924, 1928); Faustino (1927); Thiel (1932); Yabe, Sugiyama & Eguchi (1936); Crossland (1938, 1952); Stephenson & Wells (1955); Searle (1956); Nemenzo (1959); Ma (1959); Pichon (1964); Scheer & Pillai (1974); Chevalier (1975).

Merulina crispa Dana, 1846; Quelch (1886); Faustino (1927).

Figs. 358-365 *Merulina ampliata* (× 0.65).

Fig. 358 From Tijou Reef.
Fig. 359 From Bowden Reef.
Fig. 360 From Eyre Reef, collecting station 19.
Fig. 361 From Frigate Cay, Swain Reefs, collecting station 81.
Fig. 362 From Bushy Island-Redbill Reef, collecting station 80.
Fig. 363 From Yorke Island, collecting station 13.
Fig. 364 From the Pompey Complex, collecting station 75.
Fig. 365 From Low Isles, collecting station 12.



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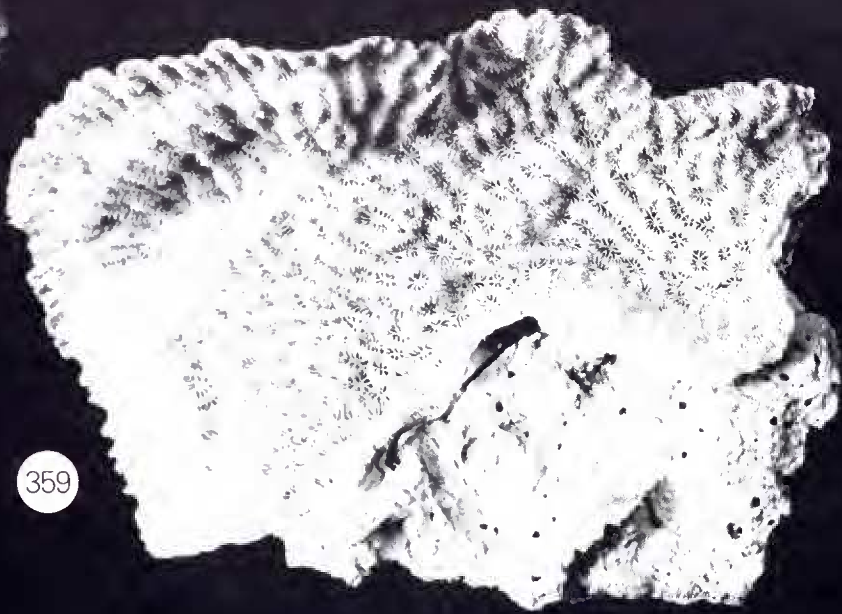

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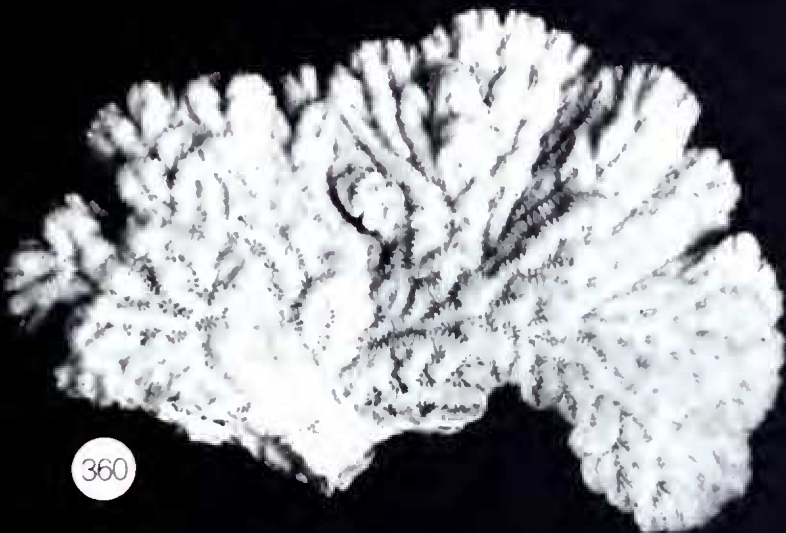

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Merulina regalis Dana, 1846; Verrill (1864); Ortmann (1888); Studer (1901); van der Horst (1921); Ma (1959).

Merulina speciosa Dana, 1846; Verrill (1864).

Merulina ramosa Edwards & Haime, 1851a; Edwards & Haime (1857); Duncan (1886); van der Horst (1921).

Merulina vaughani van der Horst, 1921; Hoffmeister (1925); Faustino (1927); Nemenzo (1959).

It seems probable that three of Dana's *Merulina* species are synonyms of *M. ampliata*. *Merulina speciosa* from Fiji consists of a compact mass of thin, twisted, anastomosed fronds which are mostly unifacial. The walls are comparatively thick, especially in relation to the fineness of the fronds. The base of the specimen is expanded and more *ampliata*-like. It may be noted, however, that no *M. ampliata* from the Great Barrier Reef has been found possessing such flattened frond-like branches and none are unifacial. *Merulina crispa* is close to *M. speciosa* but corallites are more superficial and walls thinner. *Merulina regalis* is also thin walled and does not differ substantially from specimens in the present series. *Merulina vaughani* is primarily a folded cup-shaped corallum with branches starting to develop in the centre. Van der Horst (1921) noted that 'this specimen agrees exactly with Dana's description of his *M. ampliata* but . . . differs entirely from Vaughan's figure of *M. ampliata* Ellis et Sol'. Both specimens are, however, the one species, displaying the two basically different growth forms described below.

Material studied

Yorke Island, Murray Islands (2 specimens), **Thursday Island, Great Detached Reef** (2 specimens), **Tijou Reef** (5 specimens), **Bewick Island, Lizard Island** (2 specimens), **Eyrie Reef, Hope Island** (2 specimens), **Low Isles** (5 specimens), **Wheeler Reef, Bowden Reef, Palm Islands** (29 specimens), **Whitsunday Islands, Bushy Island-Redbill Reef** (2 specimens), **Pompey Complex** (6 specimens), **Frigate Cay, Swain Reefs** (3 specimens), **Heron Island**.

These localities include collecting stations 2, 5, 12, 13, 19, 22, 26, 34, 37, 42, 43, 45, 54, 55, 57, 58, 60, 67, 69, 71, 75, 79, 80, 81, 91, 98, 99, 105.

Previous records from Eastern Australia

Low Isles, Yonge (1930, 1940), Stephenson *et al.* (1931), Manton (1935), Crossland (1952), Stephenson & Wells (1955); **Heron Island**, Salter (1954).

Characters

In the manner of *Hydnophora exesa* (see Veron *et al.*, 1977, p. 130), this species exhibits a wide range of growth forms which are not ecomorphs, but a result of sequential growth stages largely independent of environmental influence. Initially, colonies consist of laminar, encrusting, or horizontal plates. Most subsequent horizontal growth, even in large colonies, has the form of these plates (Fig. 764) and large colonies usually have a perimeter of plates which have an irregular appearance or consist of overlapping tiers. Some colonies consisting only of horizontal plates attain diameters of several metres (Fig. 374). In most, however, the central part of the initial plate becomes hillocky with the hillocks subsequently developing into branches (Fig. 372). These branches are initially short and blunt and have irregular shapes. With subsequent growth they expand, divide and become highly anastomosed. When fully developed, branches may be up to 20 cm long and obscure the underlying horizontal plates. In all specimens of the present series branches are bifacial.

Fig. 366 ▲

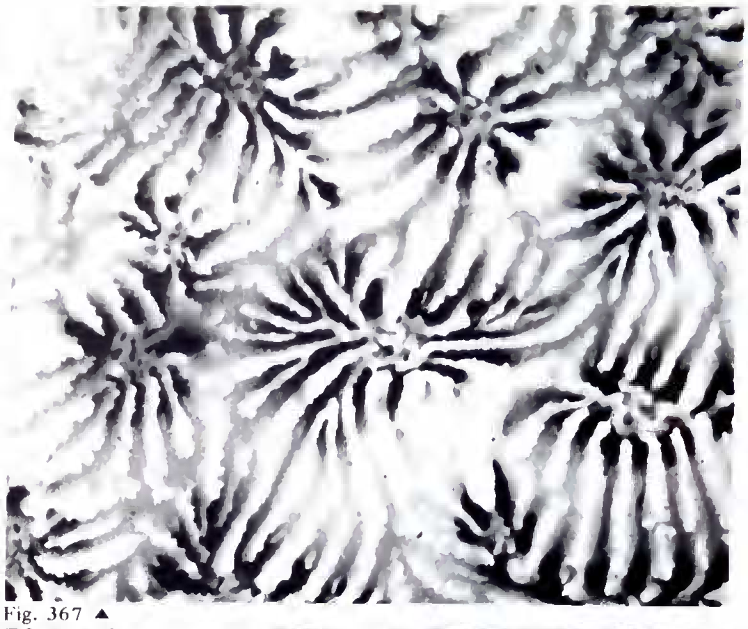

Fig. 367 ▲

Fig. 368 ▲

Fig. 369 ▲

Fig. 370 ▼

Fig. 371 ▼

Valleys generally radiate from the centre of horizontal plates and are thus perpendicular to the plate margins. They diverge and converge in an irregular manner and may be short or long (1-10 centres), long valleys (Fig. 366) occurring on flat or convex surfaces and in areas where horizontal growth is rapid. Branches may also have long or short valleys which subdivide according to the frequency of branching. Most branches have flattened ends, contorted into different shapes by the development of sub-branches and by the fine walls of developing valleys.

Septa are in two alternating orders. First order septa are usually inclined towards plate perimeters or branch ends. They are regularly exsert with those of adjacent valleys adjoined over the walls except on contorted branches. They are very strongly dentate, the dentations frequently being compound and always granulated as are the septal sides. Paliform lobes may be developed, although these seldom form a conspicuous ring. Centres are spaced, both on branches and plates, at intervals of 3-7 mm. In some coralla, they are primarily separated by first order septa traversing the valleys, although in most they are separated by laminar linkages which are usually partly fused into a central columellar ridge running lengthwise along the valleys. Up to 15 septa radiate from the centres. These may have free inner margins (in which case paliform lobes are usually developed) or may be fused with the columellae, or there

Figs. 366-371 *Merulina ampliata*, Figs. 366-369 (× 5.0).

Fig. 366	From Tijou Reef, same corallum as Fig. 358.
Figs. 367, 368	From Bowden Reef, same corallum as Fig. 359.
Fig. 369	From Eyrie Reef, same corallum as Fig. 360.
Fig. 370	From Yorke Island, same corallum as Fig. 363 (× 1.0).
Fig. 371	From Low Isles, same corallum as Fig. 365 (× 1.0).

Fig. 372 *Merulina ampliata* from the Swain Reefs.

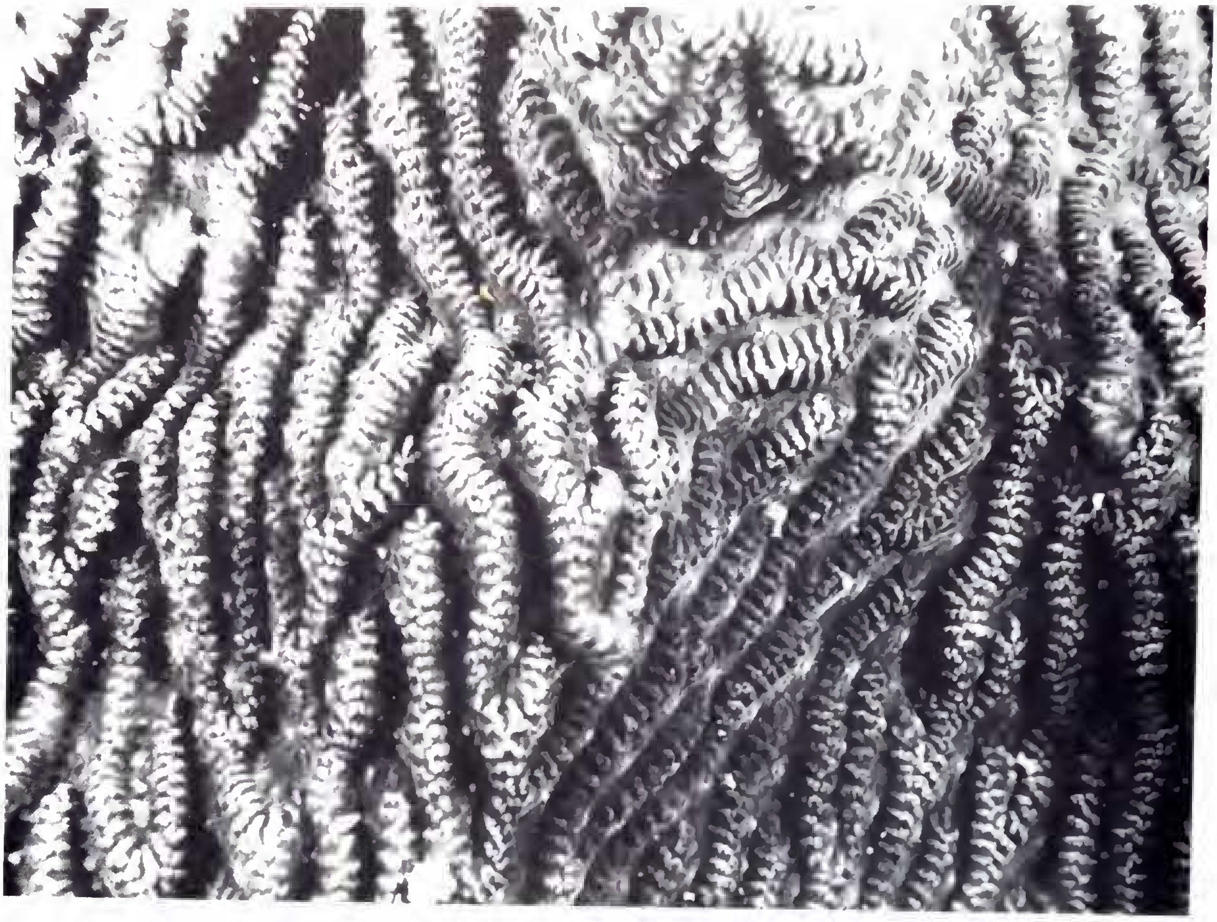

Fig. 373 *Merulina ampliata* from the Palm Islands, with polyps retracted during the day.

Fig. 374 *Merulina ampliata* from Lord Howe Island.

may be some irregular fusion between the inner margins of the longest septa. Second order septa are abortive. If developed, they are much smaller than those of the first order and frequently consist only of a series of spines. Columellae near the tips of branches consist primarily of elongate, twisted dentations. Elsewhere they are spongy or fused into one unit along with the inner margins of the primary septa.

Living colonies have a variety of pale colours, usually cream or pale brown.

Affinities

The plate-like expansions at the base of *Scapophyllia cylindrica* may be confused with *M. ampliata* but are distinguished by having better defined centres with more inclined septa and outwardly expanding valleys. Although whole colonies of these genera have very differing growth forms, their calicular characters clearly indicate close affinity.

Merulina ampliata is also close to *Clavarina scabricula* (which has not been found in the Great Barrier Reef). Chevalier (1975) noted that the latter is distinguished by greater isolation of the calices, by greater development of vertical paliform lobes and by larger valleys. Matthai's (1928) figure (Plate XV, Fig. 4) of what is probably Dana's type indicates a greater degree of branching than found in any specimens of the present series. Unknown to Matthai, however, *C. scabricula* can have a laminar base. This led Umbgrove (1940) and Chevalier (1975) to include it in *Merulina*, with *M. ampliata*.

Occasionally, heavily calcified *M. ampliata* plates (Fig. 367) closely resemble various faviid genera, e.g. *Goniastrea* and *Platygyra*, which further emphasises the close affinity of these families (see Fig. 1).

Distribution

Widely distributed from the Red Sea and western Indian Ocean to the Pacific east to Tonga and Samoa.

GENUS *CLAVARINA* VERRILL, 1864

Generic synonymy

Clavarina Verrill, 1864; Vaughan & Wells (1943); Wells (1956).

Type species *Merulina scabricula* Dana, 1846.

Introduction

The genus *Clavarina* has previously been known from two nominal species (*C. scabricula* Verrill, 1864 (Fig. 385) from Fiji and *Merulina togianensis* Umbgrove, 1940 (Fig. 386) from the Celebes) which are probably synonyms (see below, p. 227).

Umbgrove (1940) and Chevalier (1975) discussed the relationships between *C. scabricula* and *Merulina ampliata* and both concluded that these species belong to the same genus, *Merulina*. However, the addition of a third species, described below, which is clearly not a *Merulina*, but is related to *C. scabricula*, necessitates a revival of *Clavarina* as a separate genus.

Characters of the genus

Clavarina is like *Merulina* but is primarily or entirely ramose.

Clavarina triangularis n. sp.

Material studied

Yorke Island, Yonge Reef, Lizard Island (4 specimens), **Ribbon Reef, Low Isles, Bowl Reef, Palm Islands** (18 specimens), **Broadhurst Reef** (2 specimens), **Whit-**

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sunday Islands (2 specimens), **Bushy Island-Redbill Reef** (2 specimens), **Pompey Complex** (2 specimens), **Swain Reefs** (2 specimens).

These localities include collecting stations 3, 10, 11, 12, 13, 45, 55, 65, 71, 72, 73, 75, 79, 91, 97, 100, 102.

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies, which frequently exceed 1 m diameter, resemble those of *Hydnophora rigida* in consisting entirely of a network of anastomosing branches without any plate-like or foliaceous basal attachment (Figs. 765, 766). Some colonies have lax, open branching, while others are compact and bushy. Old branches may be up to 1.5 cm thick; most average 1 cm except towards the tips where they taper. All branches are basically triangular in section and have three series of centres, one on each side, with the angles being the common walls. On most branches the series of centres are straight and divide only when the branch divides. Thicker branches may have more irregular series with frequent divisions not associated with sub-branches and branch sections may be more circular than triangular. Branch tips (Figs. 381, 382) are three-pointed star-shaped in section, with the centres lying along the valleys and the walls forming the points. Septa are in two alternating orders. First order septa are slightly exsert, either adjoined over the wall or, more usually, separated by a groove. They increase in thickness towards the 'valley' axes and most curve towards the nearest centre. Their inner margins, which are mostly vertical, may have large dentations. However, most skeletal structures at the centres and along the valley axes are fused together so that the centres are star-shaped, consisting of 5-10 thick, radiating septa with fused inner margins and deep inter-septal loculi (Fig. 383). Second order septa are short and usually thinner than those of the first order. All septa are dentate, those of the first order usually more so than those of the second. Centres are linked by a single, sometimes very thick, laminar plate, which itself is fused to adjacent septa. There are no clearly defined calices and valleys are often very superficial. Columellae may be trabecular or spongy, but are only distinguishable as such near branch tips.

Individual centres and the perimeter of oral discs are clearly defined in living coralla. When polyps are expanded at night, fine, elongate tentacles usually occupy most of the space between the branches. Colonies are pale yellow or cream.

Skeletal variation

Large colonies usually have compact, frequently anastomosing branches giving the colony a bushy appearance. Such colonies are readily broken by wave action and daughter colonies, growing from scattered fragments, frequently have irregular shapes. However, most of the species variation in skeletal structure can frequently be found in the one corallum or branch. Older parts of branches are usually heavily calcified with valleys indistinguishable and centres distinguished only as star-like radiating septa as described above. Valleys become more apparent towards the branch tips where septal dentations become trabecular and the elements of spongy columellae discernible.

Figs. 375-379 *Clavarina triangularis* (× 0.5).

Figs. 375, 379 From Bushy Island-Redbill Reef, collecting station 73, Fig. 375 the holotype.
Fig. 376 From the Swain Reefs, collecting station 79.
Figs. 377, 378 From the Pompey Complex, collecting stations 71 and 72 respectively, both paratypes.

Affinities

Clavarina triangularis has clear affinities with both the Faviidae and the Merulinidae. With the Faviidae, there has long been confusion between *Hydnophora rigida* and the genera *Merulina* and *Clavarina* (see p. 216). The general appearance of *H. rigida* is similar to that of *C. triangularis*, and there is close similarity between the star-shaped centres at the base of *C. triangularis* branches and the flattened monticules at the base of *H. rigida* branches. The branch ends of both species, likewise, show similar septal and columella structures.

Figs. 380-383 *Clavarina triangularis* (× 5.0).

Figs. 380, 381 From Bushy Island-Redbill Reef, same corallum as Fig. 379, showing the appearance of anastomosed branches and branch tips respectively.

Figs. 382, 383 Same corallum from Orpheus Island, Palm Islands, collecting station 91, showing a branch tip and fused side respectively.

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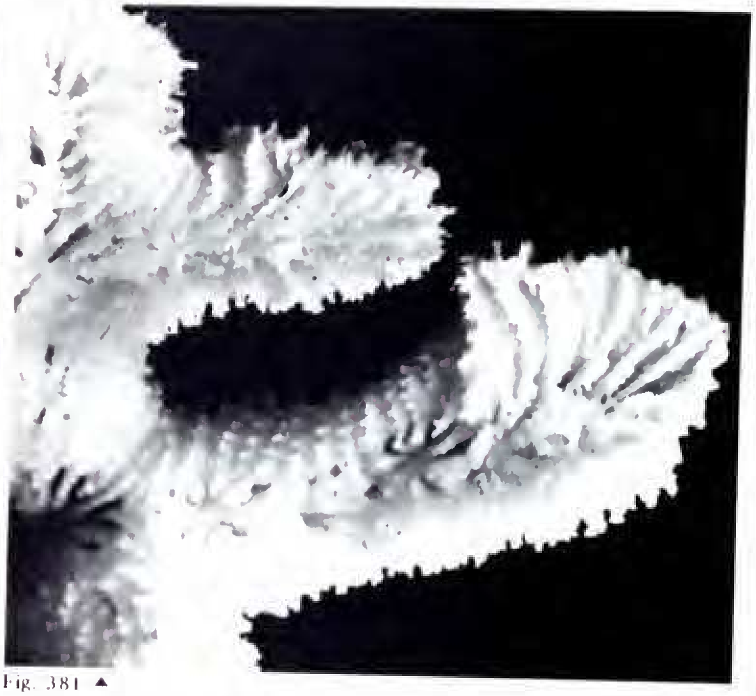


Fig. 381 ▲

Fig. 382 ▼

Fig. 383 ▼

Fig. 384 *Clavarina triangularis* from the Palm Islands, with polyps retracted during the day.

Within the Merulinidae, *C. triangularis* is closest to *M. scabricula* Dana (the type species of *Clavarina* Verrill) and to *M. togianensis* Umbgrove, a probable junior synonym of *scabricula*. Without the present species, there would appear little reason for maintaining *Clavarina* separate from *Merulina*, and most authors have not done so. However, as *C. triangularis* can hardly be placed in *Merulina* and as it does have clear affinities with *C. scabricula*, the authors propose to revive the genus *Clavarina* rather than create a new genus for *triangularis*.

Branching *C. scabricula* coralla, or parts of coralla, are similar to those of *C. triangularis* in having similarly alternate septa with similar dentations. They differ in having deeper, better defined calices with paliform lobes and in having branches with irregular numbers of series. Thus, *C. scabricula* may have flattened or irregularly shaped branches, which are clearly distinct from the three-sided branches of *C. triangularis*.

Etymology

Named because of the triangular cross section of branches.

Holotype (Fig. 375)

Dimensions: 27 cm wide, 14 cm high.

Locality: Bushy Island-Redbill Reef, collecting station 73.

Depth: 5 m.

Collector: J.E.N. Veron.

Holotype: British Museum (Natural History).

Paratypes (Figs. 377, 378)

Fig. 377. Queensland Museum, Australia.
Fig. 378. Australian Institute of Marine Science.

Distribution

Known only from the Great Barrier Reef.

GENUS *SCAPOPHYLLIA* EDWARDS & HAIME, 1848

Generic synonymy

Scapophyllia Edwards & Haime, 1848c; Matthai (1928); Vaughan & Wells (1943); Wells (1956); Chevalier (1975).

Fig. 385 Holotype of *Clavarina scabricula* (× 5.0).
Fig. 386 Holotype of *Clavarina togianensis* (× 5.0).

Fig. 385 ▼

Fig. 386 ▼

Type species *Scapophyllia cylindrica* Edwards & Haime, 1848c.

Characters of the genus

Scapophyllia is like *Merulina* but is massive-columniform.

Scapophyllia cylindrica (Edwards & Haime, 1848)

Synonymy

Scapophyllia cylindrica Edwards & Haime, 1848c; Edwards & Haime (1857); Matthai (1928); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1940); Searle (1956); Ma (1959); Scheer & Pillai (1974); Chevalier (1975).

Merulina studeri Bedot, 1907; van der Horst (1921).

Material studied

Murray Islands (2 specimens), **Sue Island** (3 specimens), **Jewell Reef** (4 specimens), **Lizard Island** (4 specimens), **Eyrie Reef** (3 specimens), **Yule Reef, Palm Islands** (4 specimens), **Pompey Complex** (5 specimens).

These localities include collecting stations 15, 63, 64, 80, 93, 95, 97, 120, 124, 135, 136, 138, 139, 164, 166, 167, 168.

Previous records from Eastern Australia

Not previously recorded.

Figs. 387-390 *Scapophyllia cylindrica* (× 5.0).

Fig. 387 From a barrier reef near Yule Entrance.
Fig. 388 From Barber Island, Palm Islands, collecting station 93.
Figs. 389, 390 From Jewell Reef, collecting station 61.

Fig. 387 ▼

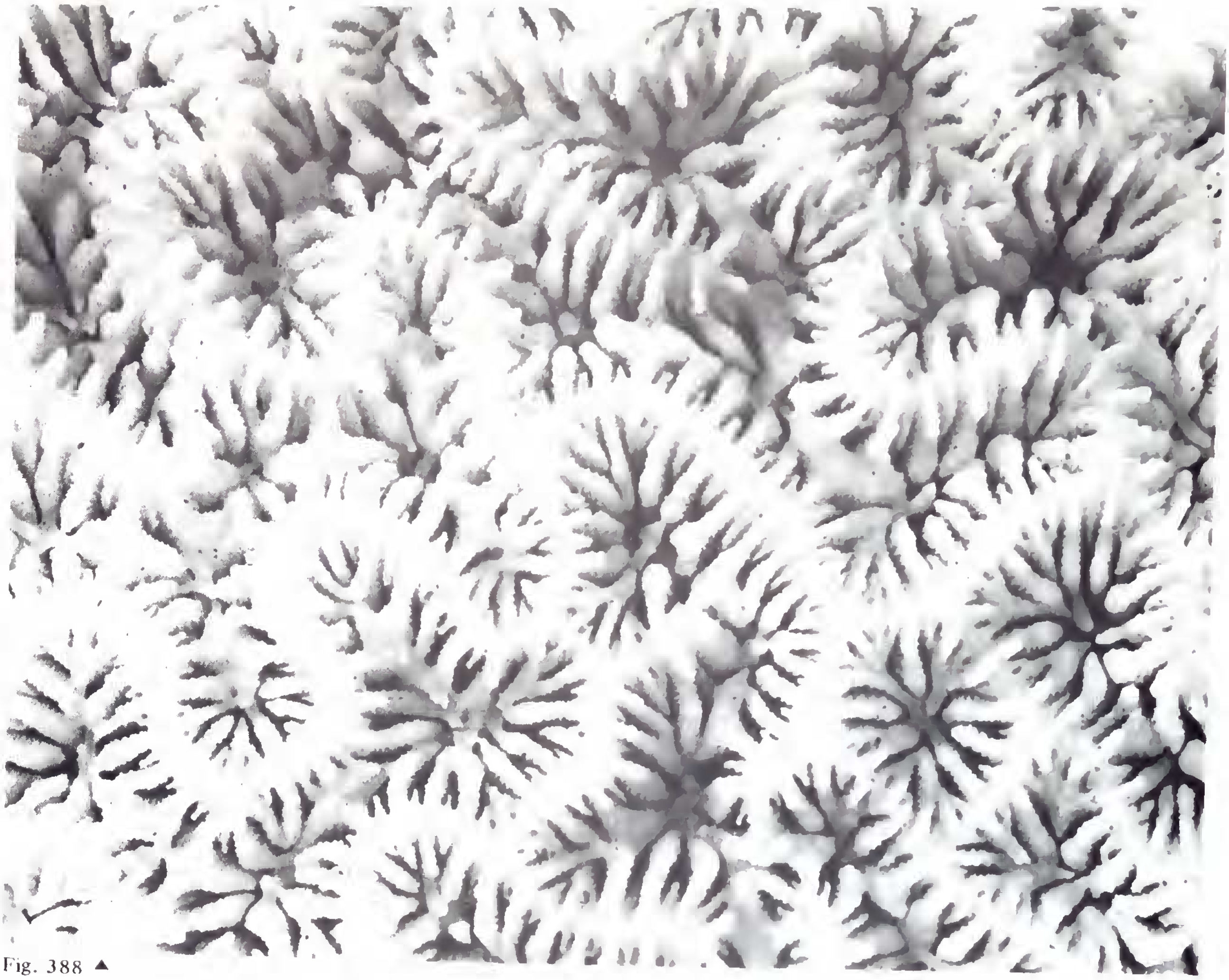
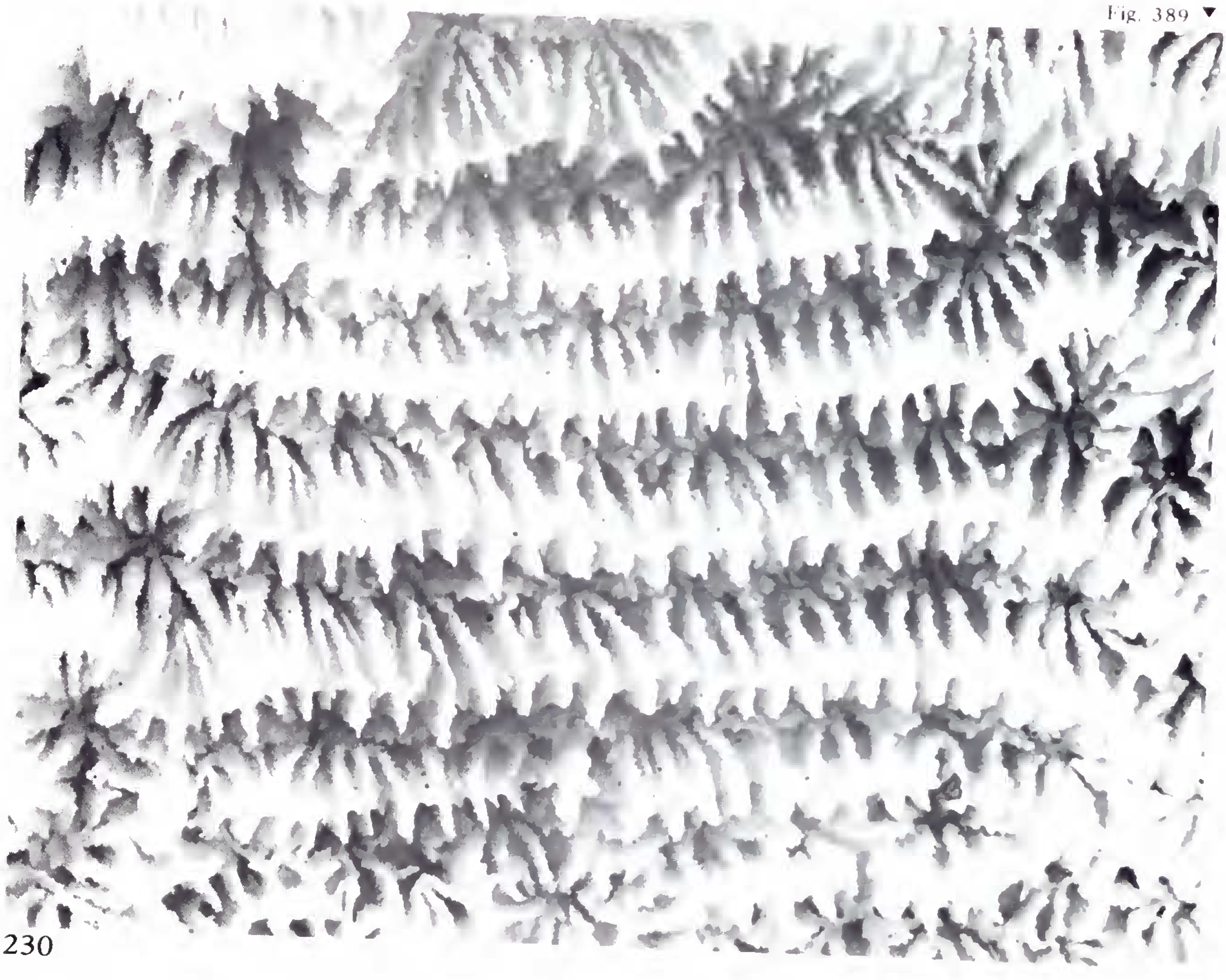


Fig. 388 ▲

Fig. 389 ▼

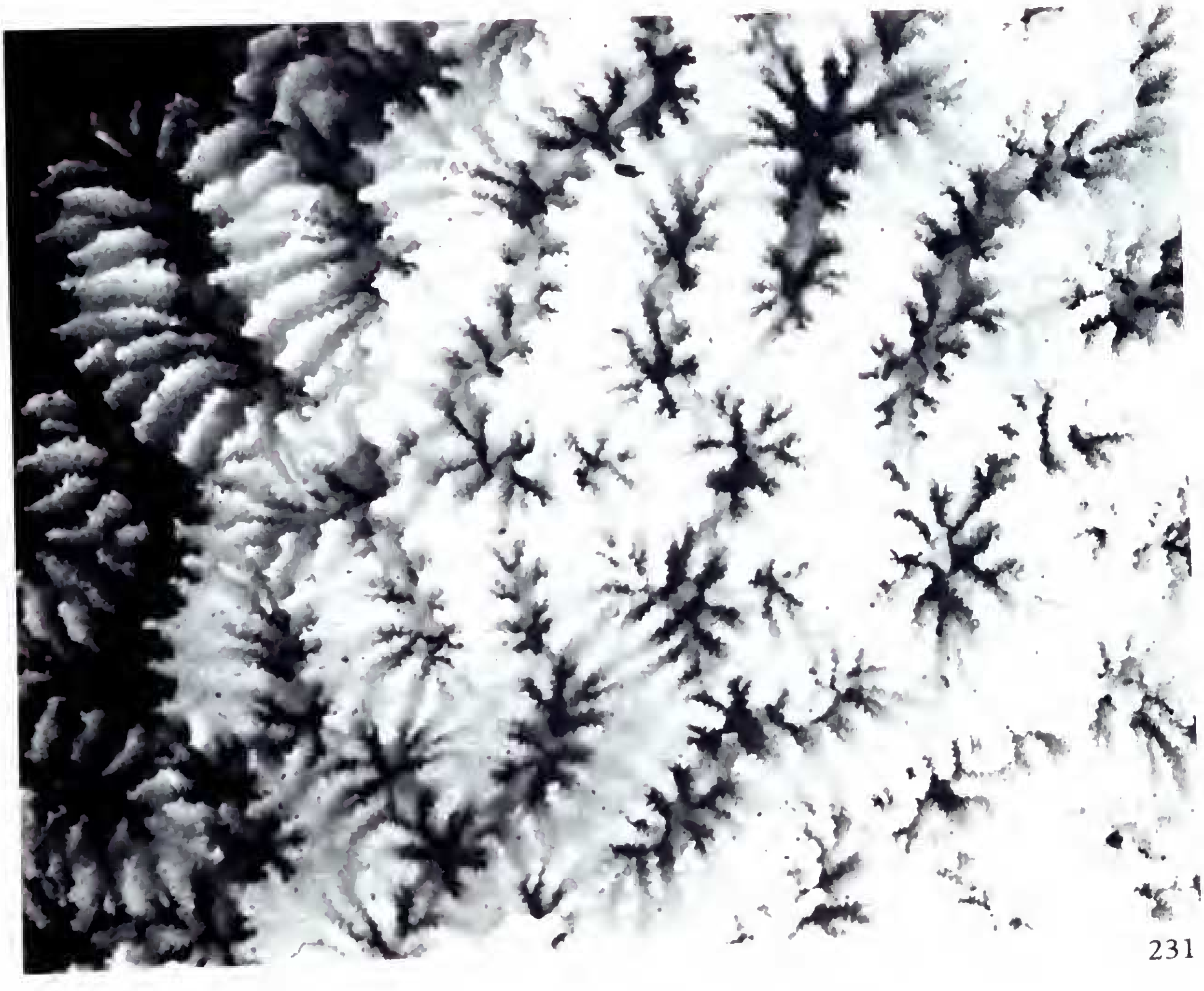


Characters

Large colonies consist of vertical, blunt-ended columns (frequently > 15 cm thick and up to 60 cm high), based on thick laminar plates. Some colonies consist mostly of columns while others, especially young ones, consist mostly of encrusting plates. Columns may divide into two or more vertical sub-branches which do not anastomose. Plates usually have irregular shapes and uneven upper surfaces. Valleys are usually sinuous on columns but may be straight and parallel on plates where they run perpendicular to the margin. They are usually 1.5-3 mm wide and up to 3 mm deep. Septa are in two alternating orders. First order septa are irregular in shape, although evenly exsert. Those of adjacent valleys are not usually adjoined, except when valleys are straight and parallel. Sometimes there is a very fine ridge over the wall. First order septa become greatly thickened towards the valley floor where they form thick horizontal elements curved towards the centres or fused with the columellae. Second order septa are not exsert and are narrower and thinner, usually tapering towards the valley floor. All septa are irregularly granulated. Centres are usually distinguished by the thickened first order septa which converge towards them. Discrete columellae may be present, composed of elongate, twisted inner septal dentations, which may be greatly thickened. Most coralla have continuous columellae composed of thickened septa, septal dentations and laminar linkages fused into a single irregular unit. Walls vary greatly in thickness, with the full range of variation frequently occurring in the one corallum. They are usually much thicker on convex surfaces than concave ones. The edge zones of laminar plates are usually narrow (< 1 cm), costate and regularly undulated or fluted.

Living colonies are cream or yellow-brown in colour. Tentacles are long and tapering and are expanded only at night.

Fig. 390 ▼



Skeletal variation

Apart from variation due to differing degrees of plate-like and column-like growth, there is very little growth form variation in this species. Columns are predominant in shallow reef biotopes while plates predominate in more turbid biotopes. All skeletal elements show a wide range in degree of calcification, frequently in the one corallum. This species is seldom seen in protected biotopes associated with turbid water.

Distribution

Scapophyllia is restricted to the central tropical Indo-Pacific from Malaya and Sumatra in the west to the Marshall Islands in the east and the Great Barrier Reef and New Caledonia in the south.

Dana (1848) gave a re-description of *Mussa* to include 16 nominal species from both the Atlantic and Indo-Pacific. The genus was then restricted to non-meandroid forms by Edwards & Haime (1857) who included some 20 species in it. Vaughan (1918) designated *Madrepora angulosa* Pallas from the West Indies as type species and the genus has since been restricted to the Atlantic Ocean. Since Matthai (1928), Indo-Pacific species previously referred to *Mussa* have been divided amongst *Lobophyllia* and *Symphyllia* and the usage of these genera has not since changed. The only confusion at generic level has been with the solitary genera, as described above. At specific level, the very large number of earlier nominal species has been progressively reduced to a relatively few abundant and widespread species and, in *Lobophyllia*, a similar number of rare species, apparently with restricted distributions.

Fig. 391 *Scapophyllia cylindrica* from Aureed Island, collecting station 133, showing the common columnar growth form.

VIII
Family Mussidae Ortmann, 1890

Introduction

The Mussidae are hermatypic, solitary and colonial forms primarily characterised by septa formed of several fan systems of large, simple trabeculae, each system producing a lobate dentation. Walls are septothecate or parathecate.

Matthai (1928) and most subsequent authors (Wells, 1937; Yabe *et al.*, 1936; Vaughan & Wells, 1943) up till Wells (1964a) believed the solitary genera (*Cynarina, Homophyllia, Rhodocyathus, Protolobophyllia, Sclerophyllia* and *Scolymia*) to be immature, monostomatous forms of colonial species. Wells (1956) recognised *Homophyllia* as a distinct solitary genus and later (1964a) placed *Cynarina, Rhodocyathus, Sclerophyllia* and *Protolobophyllia* in a single genus (*Cynarina*) and recognised 3 other solitary genera, *Acanthophyllia, Scolymia* (including *Lithophyllia*) and the new *Parascolymia*, an Indo-Pacific homeomorph of *Scolymia* (see p. 242).

The colonial mussid genera have also had a complex history. The genus *Mussa* was established by Oken (1815) to include three species, *Madrepora dianthus* (Esper) (including *Madrepora lacera* Pallas), *M. fastigiata* Pallas and *M. angulosa* Pallas. The first and second of these species were subsequently referred to *Desmophyllum* and *Eusmilia* by Edwards & Haime, the third was included in their *Mussa*.

Dana (1848) gave a re-description of *Mussa* to include 16 nominal species from both the Atlantic and Indo-Pacific. The genus was then restricted to non-meandroid forms by Edwards & Haime (1857) who included some 20 species in it. Vaughan (1918) designated *Madrepora angulosa* Pallas from the West Indies as type species and the genus has since been restricted to the Atlantic Ocean. Since Matthai (1928), Indo-Pacific species previously referred to *Mussa* have been divided amongst *Lobophyllia* and *Symphyllia* and the usage of these genera has not since changed. The only confusion at generic level has been with the solitary genera, as described above. At specific level, the very large number of earlier nominal species has been progressively reduced to a relatively few abundant and widespread species and, in *Lobophyllia*, a similar number of rare species, apparently with restricted distributions.

GENUS *BLASTOMUSSA* WELLS, 1961

Generic synonymy

Blastomussa Wells, 1961; Chevalier (1975).

Type species *Blastomussa merleti* Wells, 1961.

Characters of the genus (after Wells, 1961)

'Colonial, colony formation by extratentacular budding from the edge-zone, producing small phaceloid (to cerioid) tufts of erect cylindrical corallites. Corallite walls septothecal, costate, with narrow edge-zone and delicate epitheca. Septa stout, mussoid, composed of several fan systems each forming a low, rounded, lobate tooth. Columella coarsely trabecular. Dissepiments coarsely vesicular, steeply inclined downward from the wall and rising axially. Polyps lacking organic connection in adult stage.'

There is considerable geographic variability in the characters of the genus. Coralla from the western Indian Ocean and Red Sea are cerioid or nearly so and these become increasingly phaceloid towards the eastern Indian Ocean and the Pacific.

Affinities

Two species of *Blastomussa* have been described and both are found on the Great Barrier Reef. The genus does not closely resemble any other genus of colonial mussids, especially as budding is extratentacular, whereas it is intratentacular in other genera except *Acanthastrea.* As noted by Wells, septal structures are closest to *Cynarina.*

Blastomussa merleti (Wells, 1961)

Synonymy

Bantamia merleti Wells, 1961; *non* Wells (1968).

Blastomussa merleti (Wells); Wijsman-Best (1973); Chevalier (1975).

Material studied

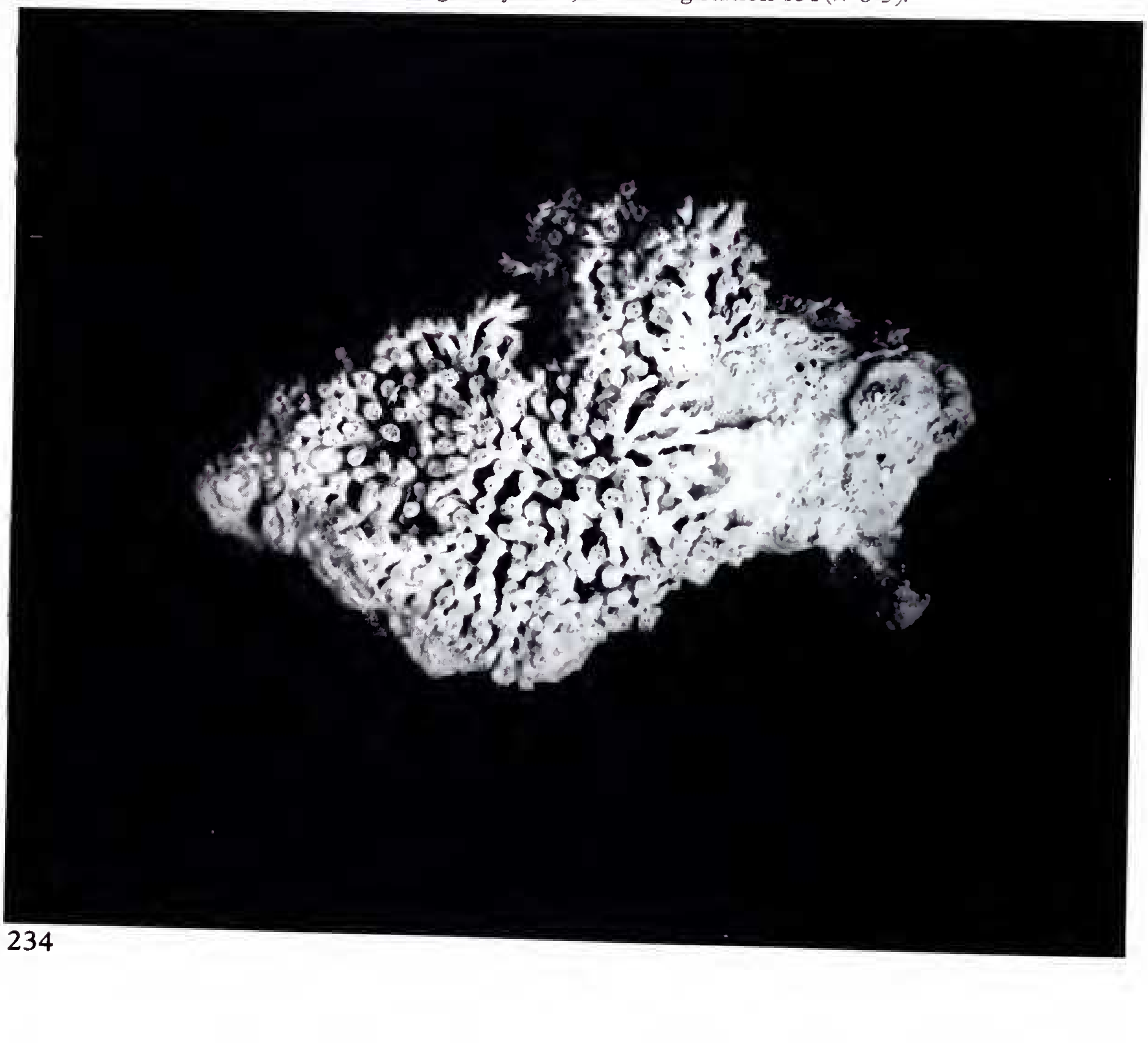
Big Mary Reef, Lizard Island (3 specimens).

These locations include collecting stations 32, 131.

Previous records from Eastern Australia

Not previously recorded.

Fig. 392 *Blastomussa merleti* from Big Mary Reef, collecting station 131 (× 0·5).



Characters

Coralla are phaceloid. Corallites are always monocentric. Budding is extratentacular with daughter corallites growing initially horizontally then becoming erect, frequently with the theca fused with that of an adjacent corallite. Corallites are up to 7 mm in diameter and are regularly spaced so that the mantle of unretracted polyps of adjacent corallites touch to form an unbroken surface of living tissues. The growing surface of colonies may be irregular with individual corallites apparently competing for space and forming daughter corallites, if space becomes available, over the top of adjacent corallites.

Septa are in three distinct cycles in smaller corallites with cycles becoming confused in larger corallites. In the former case directive septa can usually be distinguished. Septa of the first order reach the columellae, those of the second either reach the columellae or plunge vertically. Those of higher orders are reduced to fine ridges. All septa are dentate, the dentations usually arising only on their inner (sometimes vertical) margins and are not visible from above. All septa are granulated on their sides and margins. The columellae consist of fused, very coarse, septal dentations. Occasionally granulated papillae are formed. Calices are very deep with little formation of endotheca, and are thus cylindrical. Costae are hardly developed and have no ornamentation.

Wells (1961) described the polyps as being pale brown with pale yellow-green peristomes. The present specimens have a similar colour or may be dark red (Fig. 767) and these two colour combinations occur in both the Red Sea and Indian Ocean.

Figs. 393, 394 *Blastomussa merleti.*

Fig. 393 From Big Mary Reef, same corallum as Fig. 392 (× 2.5).
Fig. 394 From MacGillivray Reef, collecting station 74 (× 2.5).

Fig. 393 ▼

Polyps have fleshy maniles expanded by day but tentacles are expanded only at night, as described for *B. wellsi.*

Affinities

This species was originally placed in the family Oculinidae by Wells (1961), in the genus *Bantamia* Yabe & Eguchi, 1943. Wells later (1968) described the new genus *Blastomussa* for *B. merleti* and pointed out its affinities with the Mussidae. As noted by Wells, the septa are clearly mussid and are closest to *Cynarina.*

The two species of *Blastomussa* are readily separable on size alone but are also readily distinguished by septal structures, as described above.

Distribution

Previously recorded only from New Caledonia and Madagascar (Pichon, 1973) but is common and widely distributed throughout the Indian Ocean and the Red Sea.

Blastomussa wellsi Wijsman-Best, 1973

Synonymy

Blastomussa merleti Wells; *sensu* Wells (1968).

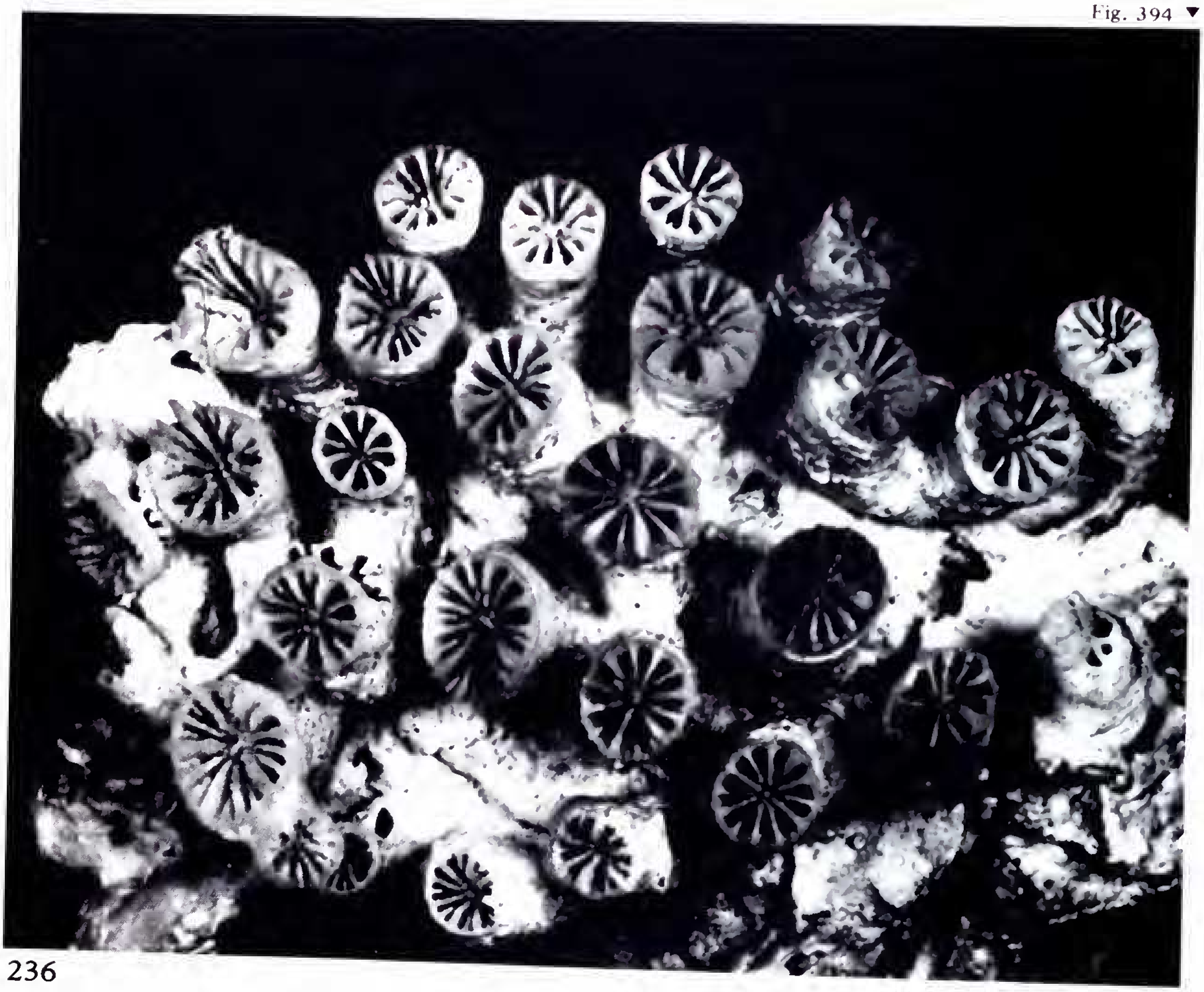
Blastomussa wellsi Wijsman-Best, 1973; Chevalier (1975).

Material studied

Yorke Island, Murray Islands (2 specimens), **Lizard Island** (5 specimens), **Palm Islands** (5 specimens), **Whitsunday Islands** (2 specimens), **Evans Head, Newcastle** (subfossil).

These locations include collecting stations 30, 32, 34, 35, 36, 98, 125.

Fig. 394 ▼



Previous records from Eastern Australia

Not previously recorded.

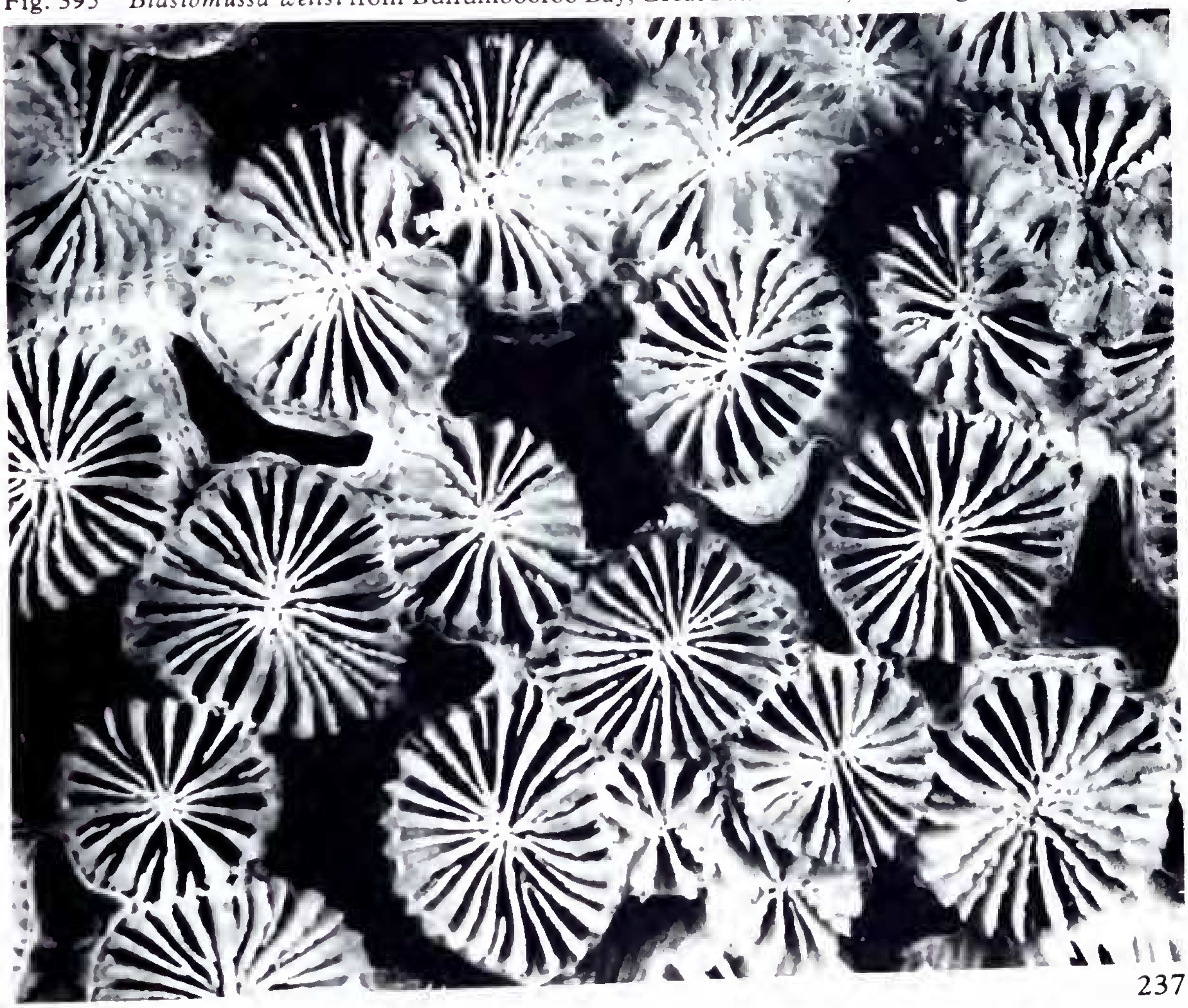
Characters

Coralla are phaceloid. Corallites are monocentric. With rare exception budding is extratentacular, or, as is the case with many coralla of the present series, successive layers of re-growth occur from the centre of corallites which otherwise appear to have died. Adjacent corallites are usually irregularly connected by epitheca, sometimes by a weakly developed common wall.

Corallites are 9-14 mm diameter. Septa are not arranged in orders. The majority are regularly exsert and extend from the thecae to the columellae, decreasing in thickness and having regular, lobate dentations which decrease in size. Major dentations are frequently separated by fine cracks which penetrate deep into the septa. Minor septa are often interspersed between major ones at the corallite periphery. The outer margins of the septa are linked by weakly developed synapticulae which is all that is developed of a theca. The epitheca is thin and weakly developed. The endotheca is also thin and weakly developed and usually consists of fine dissepiments extending outwards and upwards from the columella in the shape of a cone. Columellae are weakly developed, usually consisting of only a few twisted trabeculae.

Polyps are similar to those of *B. merleti.* Large, fleshy mantles of adjacent polyps fit compactly together giving the whole colony a uniform appearance such as might be expected from a cerioid skeleton (Figs. 768, 769). The phaceloid skeleton becomes apparent only when the polyps retract. Tentacles, however, are expanded only at night. There are two completely separate colour morphs, red and green. Both colour

Fig. 395 *Blastomussa wellsi* from Bullumbooroo Bay, Great Palm Island, collecting station 35 (× 1.0).



morphs may be found in the same biotope. There appears to be no environmental selection between them, the green morph being constantly more common. There are no skeletal differences between colour morphs.

Distribution

Previously recorded only from Noumea, and is apparently absent from the Indian Ocean.

GENUS *CYNARINA* Brüggemann, 1877

Generic synonymy

Cynarina Bruggemann, 1877b; Wells (1964).

Sclerophyllia Klunzinger, 1879.

Protolobophyllia Yabe & Sugiyama, 1935.

? *Acanthophyllia* Wells, 1937.

It is noted below that there is very little difference between the holotype of *Acanthophyllia deshayesiana* (Michelin, 1850) (the type and only species of *Acanthophyllia* Wells) and several specimens of Great Barrier Reef *Cynarina*. Present indications are that these species can be separated only on comparatively minor (specific) differences in the degree of development of paliform lobes. A study of specimens from the type locality, especially of their polyp structure, is required to confirm this conclusion.

Type species *Cynarina savignyi* Brüggemann, 1877b (= *Caryophyllia carduus* Audouin, 1826; *non Madrepora carduus* Ellis & Solander, 1786).

Characters and affinities of the genus

Only one species, *C. lacrymalis*, has been attributed to this genus and thus its characters are those of this species. Wells (1964a) distinguished *Cynarina* from other solitary mussids as follows: 'Major septa of mature coralla with non-dentate lobe on upper margins and palus-like inner lobe'. Most specimens of the present series, however, have dentate upper margins of major septa. All have a paliform lobe but this may be weakly developed. There are no other prominent differences between the holotype of *Acanthophyllia deshayesiana* (Fig. 405) and the present series of *Cynarina lacrymalis*.

Cynarina lacrymalis (Edwards & Haime, 1848)

Synonymy (partly after Wells, 1964a)

Caryophyllia carduus Audouin, 1826 (non *Caryophyllia carduus* Ellis & Solander, 1786).

Caryophyllia lacrymalis Edwards & Haime, 1848b.

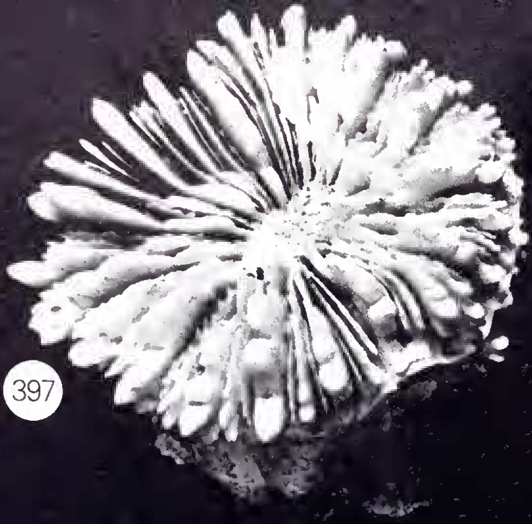
Lithophyllia lacrymalis (Edwards & Haime); Edwards & Haime, 1857.

Cynarina savignyi Brüggemann, 1877b; (*non* Brüggemann, 1877a); Klunzinger (1879); Crossland (1952).

Figs. 396-402 *Cynarina lacrymalis* (× 1.0).

Figs. 396, 400, 401, 402	From Lizard Island, Fig. 400 showing close similarity with the holotype *Acanthophyllia deshayesiana* (Fig. 405); Figs. 401, 402 showing turbinate growth forms associated with soft substrates.
Figs. 397, 399	From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.
Fig. 398	From Cateran Bay, Border Island, Whitsunday Islands, collecting station 101.

396



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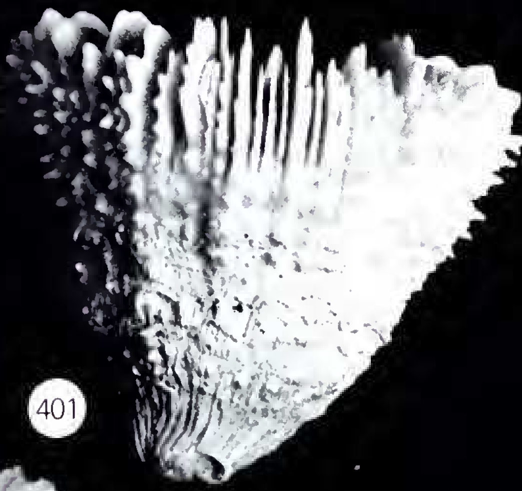
400



401

402

Sclerophyllia margariticola Klunzinger 1879; Gravier (1907, 1911); Vaughan (1907).

Lithophyllia palata Gardiner, 1899b.

Mussa (Lithophyllia) lacrymalis (Edwards & Haime) Faustino, 1927.

Antillia japonica Yabe & Sugiyama, 1931.

Antillia nemaensis Yabe & Sugiyama, 1931.

Protolobophyllia japonica Yabe & Sugiyama, 1935 (*pars*); Yabe, Sugiyama & Eguchi (1936); Ma (1937, 1959).

Protolobophyllia sinica Ma, 1959.

Cynarina lacrymalis (Edwards & Haime); Wells (1964); Utinomi (1971); Chevalier (1975).

Matthai (1928) placed *Cynarina*, along with other solitary genera, into various colonial genera on the assumption that they represented early, monocentric phases. Thus the *Scolymia, Cynarina* and *Homophyllia* of Brüggemann (1877) and the *Cynarina, Sclerophyllia* and *Mussa* of Klunzinger (1879) were all placed, questionably, in *Lobophyllia*. Wells (1937) essentially followed Matthai's opinion, while the Japanese inappropriately adopted the old genus *Antillia*, then later their new genus *Protolobophyllia*, the latter being confused with *Scolymia vitiensis*. Wells (1964a) gave a complete revision of the genus and an extensive synonymy of *Cynarina lacrymalis* which has been followed by subsequent authors.

Material studied

Darnley Island, Yorke Island (7 specimens), reef 14 km NE from **Murray Islands, Murray Islands** (3 specimens), **Aureed Island** (3 specimens), **Lizard Island** (5 specimens), **Hope Island, Low Isles, Palm Islands** (14 specimens), **Whitsunday Islands** (20 specimens), **Bushy Island-Redbill Reef** (2 specimens), **Parker Reef, Swain Reefs** (2 specimens).

These locations include collecting stations 7, 12, 13, 27, 30, 32, 34, 37, 39, 55, 59, 79, 80, 81, 90, 95, 96, 97, 98, 102, 125, 126, 133, 139.

Previous records from Eastern Australia

Low Isles (as *C. savignyi*) Crossland (1952).

Characters

Despite the complexity of the above synonymy, coralla of this species are readily recognised and the species is very distinct underwater. Coralla are monocentric, usually ovoid or circular from above, with a broad base of attachment, or are free living and turbinate (Figs. 401, 402). Septa are in three distinct orders with a fourth rudimentary order sometimes discernible. First order septa are extremely exsert with large, lobate dentations which frequently extend 10 mm above the theca. They are also very greatly thickened (up to 7 mm). Higher orders of septa are less exsert and thinner and have finer, more numerous, sometimes highly perforated dentations. All septa which reach the columellae—mostly those of the first order—form a low, broad, paliform crown. The paliform lobes are usually distinctly delineated from the rest of the septa (Fig. 398) and are themselves lobed or coarsely serrated. The sides of septa are finely granulated, and so are the septal margins, especially at the extremities of the dentations, where individual sclerodermites are usually visible. The columellae lie deep within the calice and are usually large and spongy. The endotheca is vesicular and usually little developed. The wall is almost entirely septothecate. The epitheca frequently forms regular layers over the septo-costae. The costae are very prominent and strongly dentate, those of the first order sometimes forming long, thick spines.

Living polyps are very colourful, the colours forming an endless variety of patterns which are different for each individual. The coenosarc, and frequently the oral disc, are translucent with details of the skeleton clearly visible (Figs. 403, 770 and Catala, 1964 Pl.10). The coenosarc usually forms bulbous swellings over the primary septa during the day but retracts at night as the tentacles expand. Each septum is usually associated with one tentacle except the primary septa which have two or three tentacles (Fig. 404).

Like *Plerogyra, Physogyra* and *Scolymia* species, *C. lacrymalis* is most commonly found in protected biotopes where light intensity is marginal for hermatypic corals.

Skeletal variation

Coralla from well illuminated biotopes are usually heavily calcified, especially the primary septo-costae, while those from deep or turbid water have thinner and more equal septo-costae. Those growing on steeply sloping substrates may have distorted shapes as the polyps tend to grow unevenly until the thecal rim is horizontal. Free living coralla, usually found growing on soft mud, form a distinctive ecomorph with a simple, turbinate growth form.

Distribution

Widely distributed from the northern Red Sea and Gulf of Aden to the western Pacific from Japan, New Caledonia, Loyalty Islands and Kermadec Islands.

GENUS *SCOLYMIA* HAIME, 1852

Generic synonymy

Scolymia Haime, 1852.
Lithophyllia Edwards & Haime, 1857.
Homophyllia Brüggemann, 1877b.
Parascolymia Wells, 1964a; Chevalier (1975).

Type species *Madrepora lacera* Pallas, 1766 (selected by Vaughan, 1901).

Figs. 403, 404 *Cynarina lacrymalis* from the Swain Reefs with tentacles retracted during the day (Fig. 403) and extended at night (Fig. 404).

Fig. 403 ▼

Fig. 404 ▼

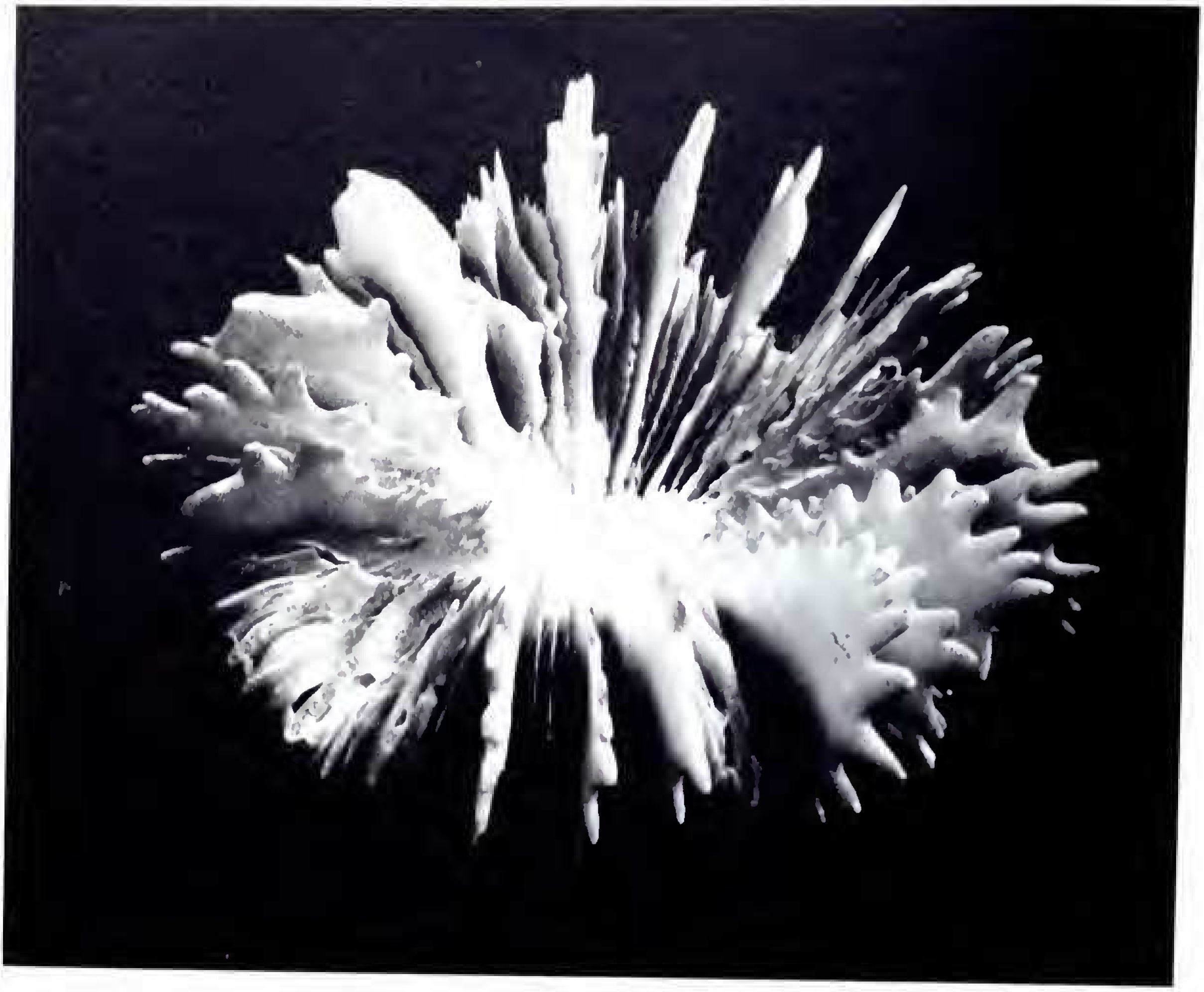


Fig. 405 Holotype of *Acanthophyllia deshayesiana* (× 1.0).

Introduction

This study indicates that species previously considered to belong to three separate genera, *Scolymia*, *Homophyllia* and *Parascolymia* are congeneric and that the latter two are synonyms with only one species involved. The first of these conclusions is discussed here, the second is discussed with the synonymy of *Scolymia vitiensis* (pp. 244).

Wells (1964a) created the monospecific genus, *Parascolymia*, for *Scolymia vitiensis* Brüggemann, with the following diagnosis and comment:

'Type—*Scolymia vitiensis* Brüggemann, 1877.

Diagnosis—like *Scolymia* Haime but asexually produced corallites with lamellar rather than trabecular linkage.

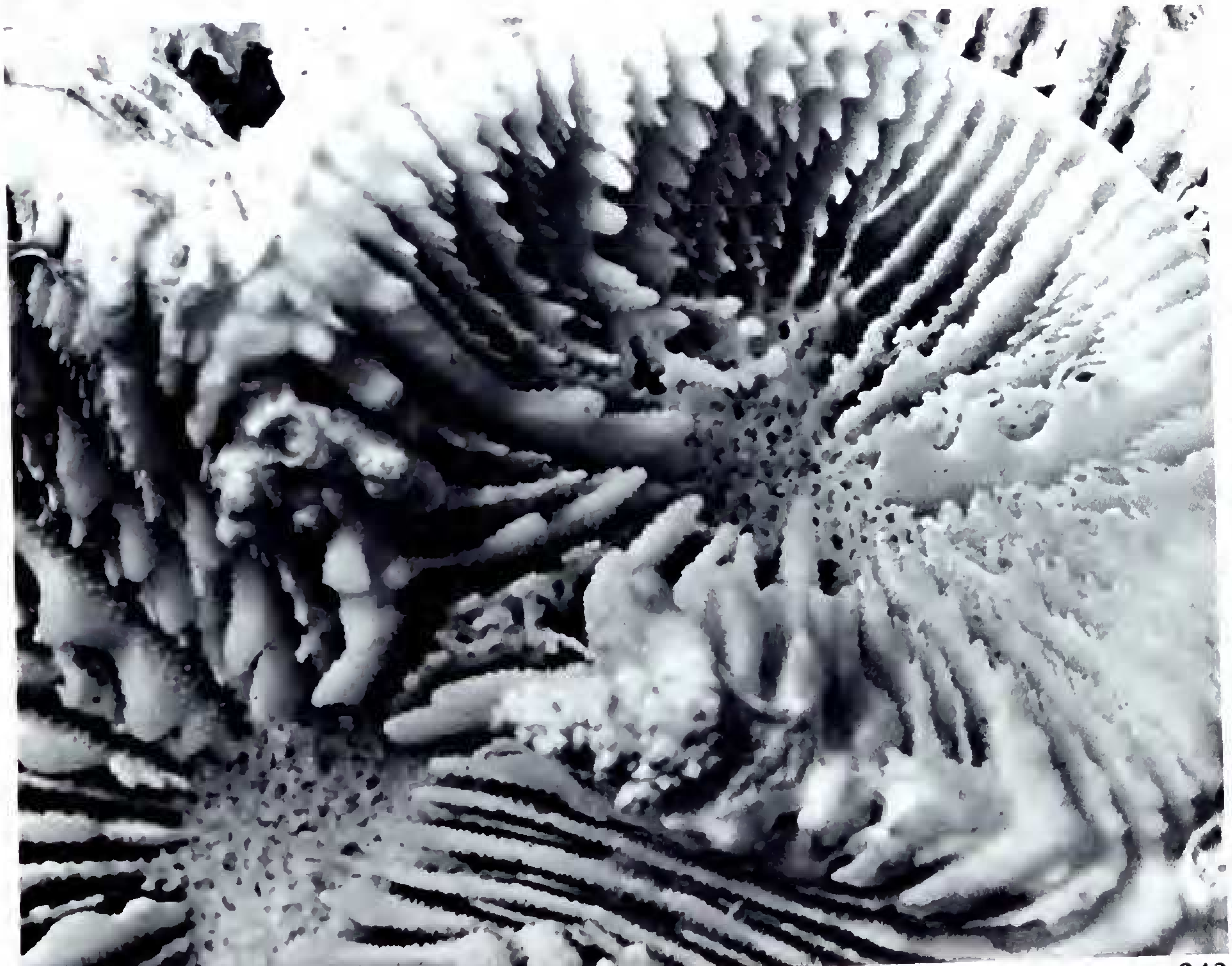
As previously noted, *Scolymia* Haime refers to the West Indian solitary mussids, and *Protolobophyllia* Yabe & Sugiyama was based on a specimen of *Cynarina lacrymalis*, hence a new name appears necessary to distinguish the Pacific homologue of *Scolymia*'. In the same paper (p. 382) Wells commented: 'As yet, the di- or tri-centric condition has not been observed in *Scolymia* to test the presumption that the linkages should be trabecular'.

The present authors believe that geographic separation is not a valid reason for creating new genera, especially as the Atlantic and Indo-Pacific have several other genera in common. Neither can (presumed) differences between linkages be used to

Fig. 406 *Scolymia cubensis* from the West Indies with two centres linked by a lamellar linkage (× 5).
Fig. 407 *Scolymia* cf. *vitiensis* from Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97, with two centres linked by a trabecular linkage (× 5).

Fig. 406 ▲

Fig. 407 ▼



separate these genera. Both genera are almost entirely monocentric. However, dicentric and tricentric *Scolymia* have been found and, as illustrated in Figs. 406 and 407, both genera have similar (lamellar or trabecular) linkages.

The monospecific genus *Homophyllia* is also included in *Scolymia* because, as described below, *Homophyllia australis* and *Scolymia vitiensis* are very similar, if not conspecific.

Scolymia cf. vitiensis Brüggemann, 1877

Synonymy

Scolymia vitiensis Brüggemann, 1877b.

Lithophyllia vitiensis Gardiner, 1899b; Crossland (1952).

Lithophyllia margariticola Folkeson, 1919.

Protolobophyllia japonica Yabe & Sugiyama, 1935a (*pars*).

Parascolymia vitiensis (Brüggemann); Wells (1964a); Chevalier (1975).

Parascolymia fungiformis Chevalier, 1975.

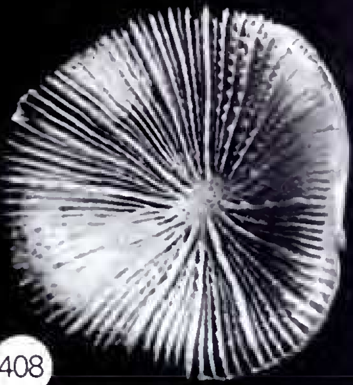
The case for synonymising *Parascolymia* with *Scolymia* has been outlined above (p. 242). At a specific level, this study shows that *Homophyllia australis* and *Scolymia* (= *Parascolymia*) *vitiensis* may form the one polymorphic species. Previous records of *Homophyllia australis* have all come from the temperate waters of southern Australia. On the basis of specimens from these localities the separation of *H. australis* from other solitary mussids, even at a generic level, would appear fully justified. However, a study was made of this species at Lord Howe Island (31° 40′ S lat.) where a full range of intermediate forms indicated that *H. australis* and *Scolymia* (= *Parascolymia*) *vitiensis* may be the same species, the former being a cold water ecomorph or geographic subspecies of the latter. Until this question is resolved experimentally, the two nominal species are retained, the name *vitiensis* (which does not have priority) being provisional only.

Chevalier (1975) distinguished his 3 specimens of *P. fungiformis* from *P. vitiensis* on the basis that the former has a convex shape, that septa are less exsert towards the calice margin, that distal septal dentations are less exsert, that granules are less abundant on the upper part of the septa, that the columella is less developed and its components less spread and that the endothecal alveoli on the external part of the calicular plateau are substantially better developed. Each of these characters is clearly developed in various coralla of the present series but they are not quantitatively associated with each other. The present series is clearly one species which displays all the variation attributed to both *P. vitiensis* and *P. fungiformis* by Chevalier.

The holotype of *S.* cf. *vitiensis* from Fiji is very close to specimens of the present series from Lord Howe Island.

Figs. 408-414 *Scolymia* cf. *vitiensis* (× 0.7).

Fig. 408 From Bushy Island-Redbill Reef, collecting station 80.
Fig. 409 From Hook Island, Whitsunday Islands, collecting station 39.
Fig. 410 From Lord Howe Island, collecting station 143.
Fig. 411 From Fantome Island, Palm Islands, collecting station 34.
Fig. 412 From Orpheus Island, Palm Islands.
Fig. 413 From the Swain Reefs, collecting station 69.
Fig. 414 From Dewar Island, Murray Islands, collecting station 29.



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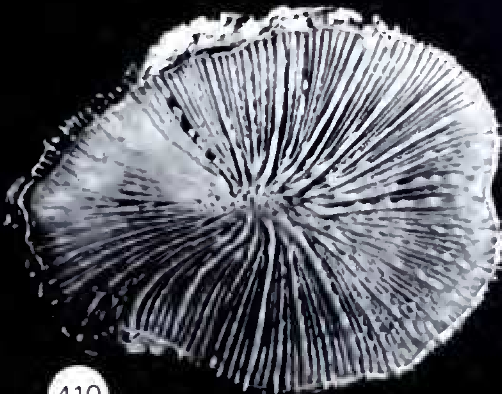

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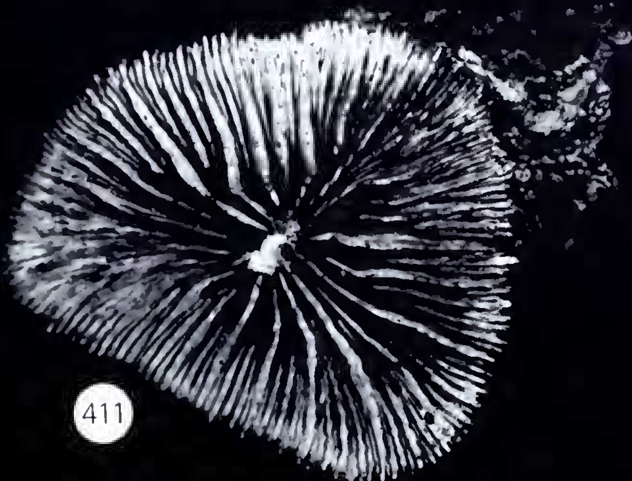

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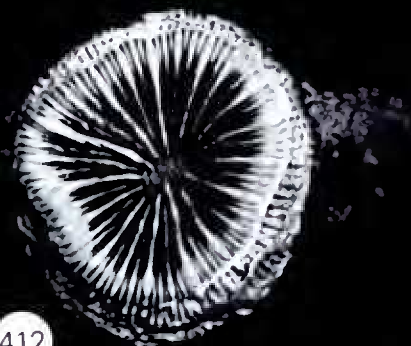

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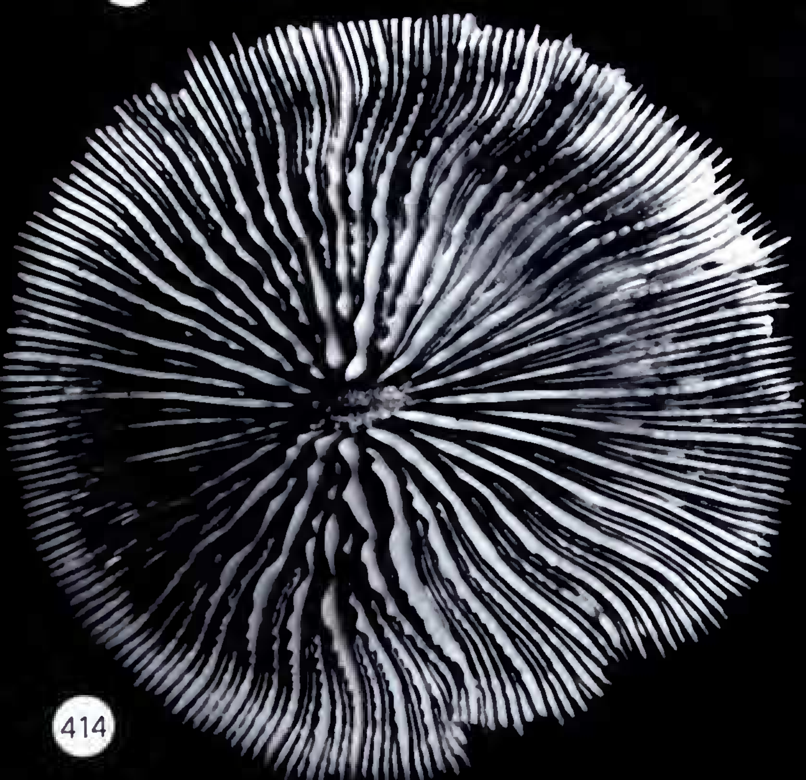

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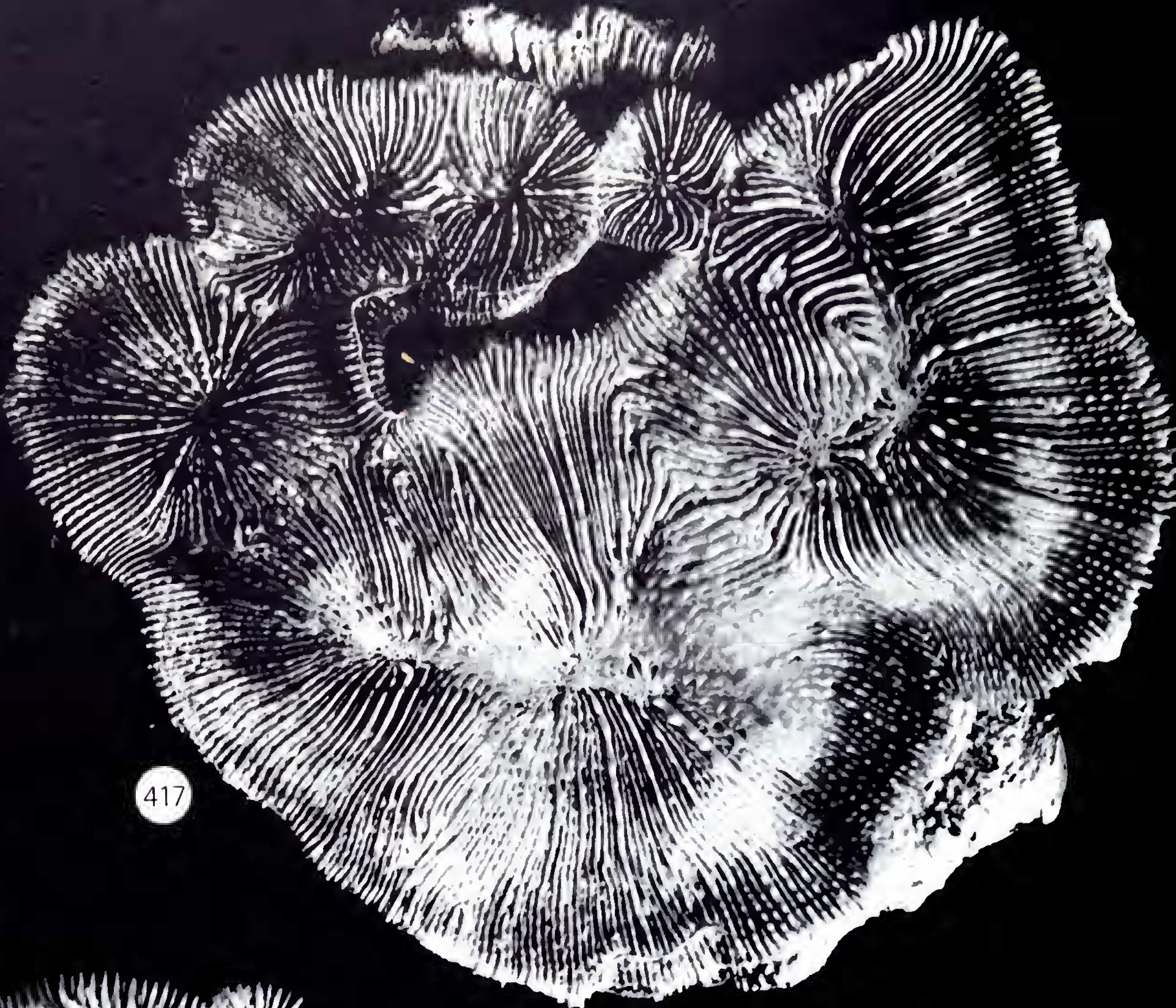

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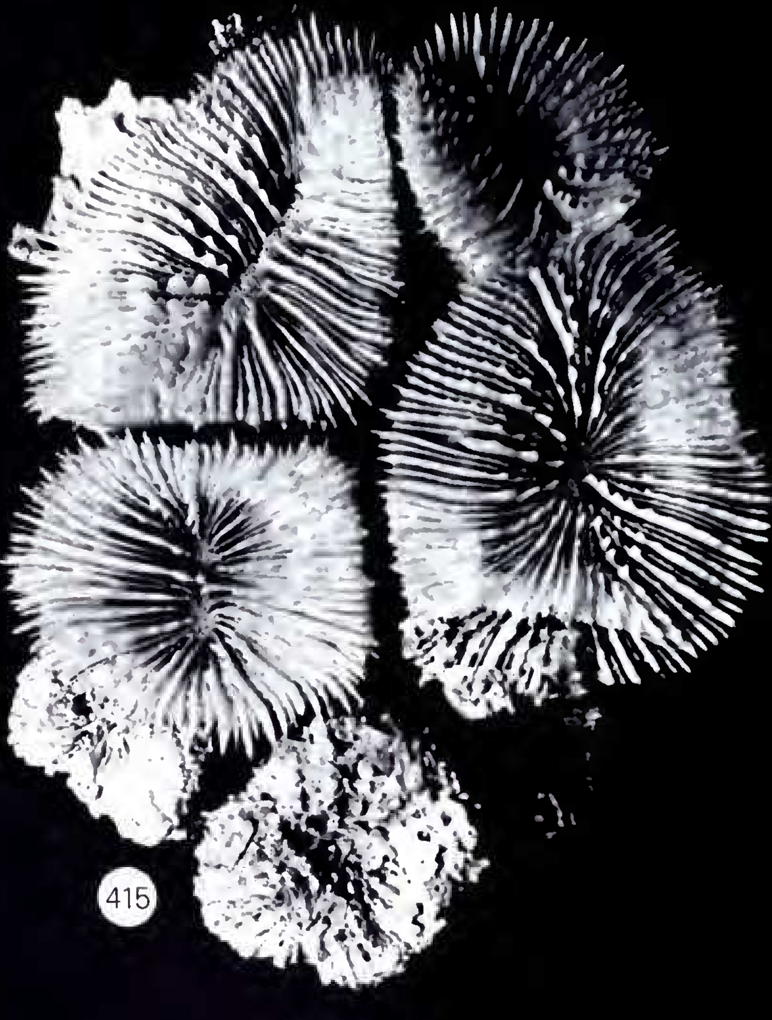

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Material studied

Anchor Cay, Darnley Island (3 specimens), **Yorke Island** (6 specimens), barrier reef 14 km NE **Murray Islands, Dungeness Reef, Murray Islands** (5 specimens), between **Murray Islands** and barrier, **Bewick Island, Jewell Reef, Lizard Island** (4 specimens), **Nymph Island, Hope Island, Low Isles, Palm Islands** (40 specimens), **Magnetic Island, Bait Reef, Whitsunday Islands** (26 specimens), **Bushy Island-Redbill Reef** (6 specimens), **Swain Reefs** (18 specimens), **Heron Island** (3 specimens), **Wistari Reef** (2 specimens), **Norfolk Island, Lord Howe Island** (49 specimens).

These locations include collecting stations 13, 27, 28, 30, 32, 33, 34, 35, 36, 37, 38, 39, 41, 42, 45, 55, 57, 58, 59, 61, 69, 76, 78, 79, 80, 81, 87, 90, 91, 92, 97, 98, 102, 108, 109, 115, 117, 123, 125, 126, 129, 142, 143, 144, 145, 147.

Previous records from Eastern Australia

Low Isles and vicinity (as *Lithophyllia vitiensis*) Crossland (1952) (as *Parascolymia vitiensis*) Wells (1964a); **Lord Howe Island** (as *Homophyllia australis*) Wells (1964a), (as *Parascolymia* sp. and *Homophyllia australis*) Veron (1974) (as *Scolymia* cf. *vitiensis*) Veron and Done (1979).

Characters and skeletal variation

The present series includes a very wide range of forms from the small solitary coralla of temperate localities, to the very large colonies of the northern Great Barrier Reef. Coralla from Lord Howe Island are described separately as they form a distinct, temperate ecomorph.

Scolymia cf. *vitiensis from Lord Howe Island* (Figs. 410, 426-431, 774).

Coralla have a wide range of size and appearance. Smaller specimens are virtually indistinguishable from those from more southern waters described as *S. australis* (below). Others have maximum diameters of up to 7 cm, and are circular, oval or irregular in outline. Five or six cycles of septa are normally distinguishable, the higher cycles decreasing in size and having finer dentations. Higher cycles sometimes fuse with lower cycles in very regular sequence. The 6th cycle costae may alternate with the first five cycles or may be equal. There is very great variation in the development of dentations, some coralla having similar dentations to those from the Great Barrier Reef, some having dentations identical to those of *S. australis*. The present series, which is very clearly a single species, includes all forms intermediate between these extremes.

Scolymia cf. *vitiensis from the Great Barrier Reef.*

Smaller specimens from tropical localities may be indistinguishable from those from Lord Howe Island. The following description, however, applies generally to coralla collected from within the Great Barrier Reef.

Coralla are commonly monocentric but sometimes become polycentric when large. In the present series, solitary coralla attain diameters of up to 14 cm while the largest colony has a maximum dimension of 21.5 cm. The upper surfaces of coralla are flat, convex or concave, with the central part of the calices (about half the septal radius) forming a shallow, conical depression. The latter character is constant in all but immature coralla. The outer margins of the conical depression may be horizontal or slope up or down giving the whole corallum a flat, concave or convex upper surface. Convex slopes are more commonly found in exposed biotopes and are associated with heavy calcification.

Figs. 415-417 *Scolymia* cf. *vitiensis* (× 0.7).

Fig. 415 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.
Fig. 416 From Great Palm Island, collecting station 92.
Fig. 417 From Orpheus Island, Palm Islands, collecting station 91.

Up to 6 cycles of septa can usually be recognized although these are seldom distinct. Septa of the first 2 cycles are conspicuously thicker than the others; they increase in thickness towards the columella or else have a constant thickness. They are strongly dentate, the dentations being very irregular in shape within the one septa, especially within the central conical depression. They are usually well developed at the rim of the conical depression of convex coralla and around the columella. Septa of higher cycles become increasingly thinner with increasingly more numerous, finer dentations. Several cycles of septa reach the columella; those that do not are either anastomosed to septa of lower cycles (except the first two cycles), or have free inner margins. The columellae are large and spongy. Their outer margins are largely composed of long, thin, highly perforated inner septal dentations of third and fourth cycle septa which cover the larger, thicker dentations of the first and second cycle.

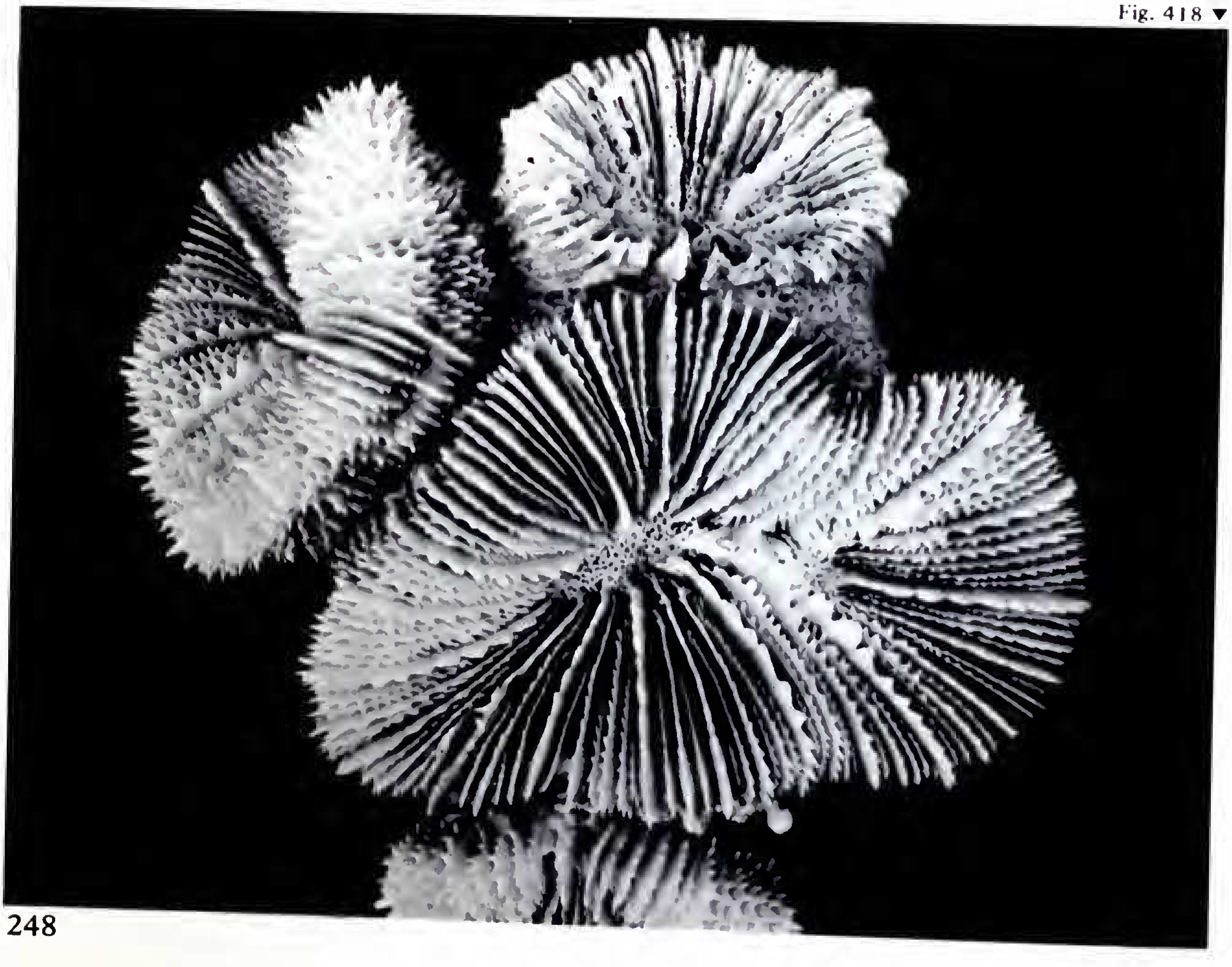
There are two distinct types of budding, both of which may occur within the one corallum. Budding may occur within the central conical depression in which case the centres are linked by laminar or trabecular linkages which have the same range of form and appearance as the septa. Thick laminar linkages are seldom anastomosed and are usually well spaced from the finer linkages. These linkages also play the same role as the septa in the formation of the columella. The second type of budding occurs at the periphery of very large, usually convex coralla. Centres are similar to those described above except in most coralla they are surrounded by a reduced number of

Fig. 418 *Scolymia lacera* from the Gulf of Mexico (× 0.4).

Fig. 419 *Scolymia lacera* from the West Indies showing skeletal structures similar to those of *Scolymia* cf. *vitiensis* (× 5).

Figs. 420-424 *Scolymia* cf. *vitiensis* (× 4.0). Fig. 420, from Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98; Figs. 421-423, same corallum from Hook Island, Whitsunday Islands, collecting station 39; Fig. 424, from Lord Howe Island, showing similar skeletal detail to *Scolymia australis* from southern Australia.

Fig. 418 ▼



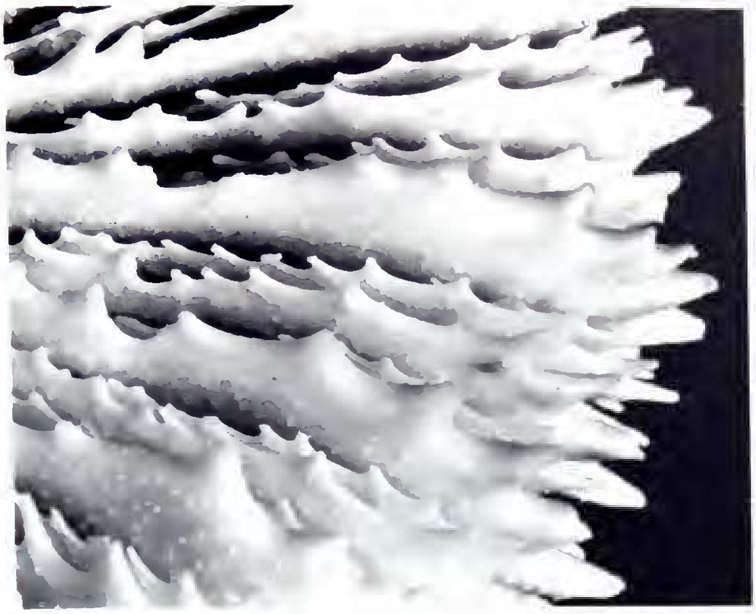


Fig. 419 ▲

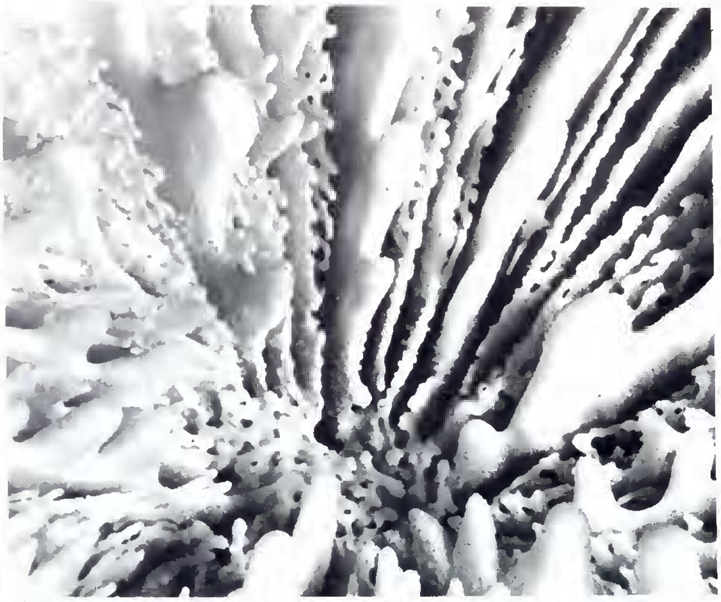


Fig.420 ▲

Fig. 421 ▲

Fig. 422 ▲

Fig. 423 ▼

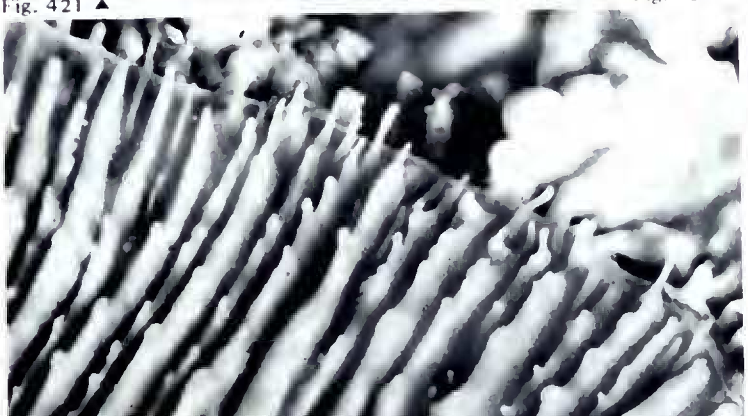


Fig. 424 ▼

greatly thickened septa, interspersed with septa of higher cycles. Septa between these centres and those of the central area are continuous; significantly there is little or no agreement as to respective cycles, thus a first order (first or second cycles) septum of a peripheral centre may be a third order septum of a central centre.

The endotheca is always vesicular, lightly calcified and least developed around thick septa or laminar linkages, or around the free inner margins of high order septa. The absence of endothecal dissepiments in such cases leads to small pits or alveoli, similar to those found in *Echinophyllia* and *Oxypora*. These alveoli tend to develop in coralla of any shape. They are most common in coralla with a relatively high proportion of septa with free rather than anastomosing inner margins. It appears that tentacles occur above the alveoli in this species (as in many *Fungia* species).

Living coralla (Figs. 771-774) have dark colours, usually green or brown. Polyps resemble *Fungia* species in being thin and non-fleshy with short, broad-based tentacles expanded at night.

Affinities

Except in relation to *S. australis,* this species cannot readily be confused with any other except in immature stages. Even then it is always clearly distinguished from *C. lacrymalis* by the latter having strongly developed dentate costae and a low, although usually clearly distinguishable, paliform crown. Immature *S.* cf. *vitiensis* are less readily distinguished from *Lobophyllia* species, especially *L. hemprichii.* The latter, however, does not have a central conical depression as described and usually has finer, more echinulate dentations which extend down the usually well formed costae.

Scolymia cf. *vitiensis* is close to the three supposed species of Atlantic Ocean *Scolymia* (see Laborel, 1967 and Wells, 1971b). *Scolymia wellsii* Laborel is a small species, up to 6 cm diameter. *Scolymia lacera* (Pallas) (Figs. 418, 419) and *S. cubensis* (Edwards & Haime) are similar in size to *S.* cf. *vitiensis.* The former is primarily distinguishable by having larger septal dentations which continue unchanged over the margins of the calice. The latter species has finer and more numerous septa, but is otherwise very similar to some *S.* cf. *vitiensis* from the Great Barrier Reef.

Distribution

Recorded from NW Australia (Folkeson, 1919) and from the western Pacific east to the Marshall Islands and Fiji.

Scolymia australis (Edwards & Haime, 1849)

Synonymy

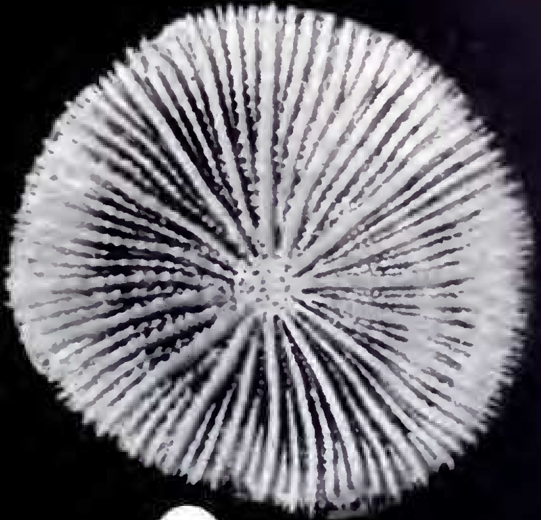
Caryophyllia australis Edwards & Haime, 1849a.

Homophyllia australis (Edwards & Haime); Brüggemann (1877b); Tenison-Woods (1878); Dennant (1904); Howchin (1909); Wells (1964a).

Culicia magna Tenison-Woods, 1878; Totton (1952).

The generic change from *Homophyllia* to *Scolymia* is discussed above (p. 242). Specimens of *Isophyllia australis* in the Paris Museum appear to be a mixture of *Isophyllia sinuosa* Ellis & Solander and *Scolymia australis.* Edwards & Haime's (1860) description applies in part to Atlantic *Isophyllia* (as does that of Quelch). The type specimens of *Caryophyllia australis* (number 865) from Port Lincoln, South Australia, which are very eroded, do not correspond to Edwards & Haime's (1849a) figure (Pl. 8, Fig. 2).

Fig. 425 — *Scolymia australis* from St Vincent's Gulf, South Australia (× 2.5).
Fig. 426-431 — *Scolymia* cf. *vitiensis* from Lord Howe Island (× 1.0). Fig. 426 from Phillip Point; Fig. 428 from Blackburn Island; Figs. 427, 429-431 from collecting stations 198, 143, 142, 147 respectively.



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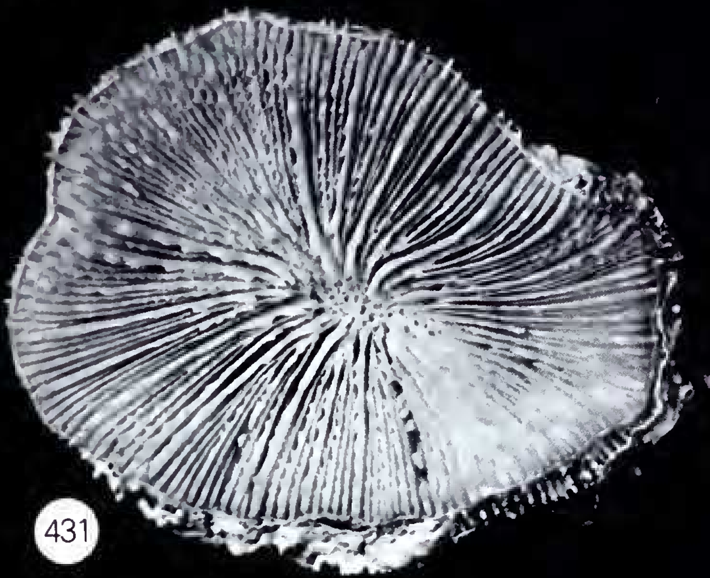


431

Material studied

Port Phillip Bay (7 specimens), **St Vincents Gulf** (4 specimens), **Spencer Gulf** (5 specimens), **Rottnest Island** (2 specimens).

Previous records from Australia (other than Lord Howe Island, see p. 242).

Port Phillip Bay, St Vincents Gulf and southern Australia (as *Culicia magna*) Tenison-Woods (1878) (as *Homophyllia australis*) Dennant (1904) (as *Homophyllia australis*) Howchin (1909) (as *Homophyllia australis*) Squires (1966).

Characters

Coralla from the south coast of Australia are shallow, solitary cups up to 2.6 cm maximum diameter (Fig. 425). Septa are in 5 complete cycles. The first two are equal, the third is slightly thinner and the dentations slightly finer. The first three cycles reach the columella, the fourth extends inward 1/2-2/3 the septal radius, the fifth extends inwards approximately 1/3 the septal radius. The higher cycles of septa become progressively thinner and more finely dentate. Fifth cycle septa usually have free inner margins, those of the third and fourth cycle may anastomose. All septa are covered with fine granulations usually arranged in trabecular rows. The columella is dense. The costae alternate in thickness, corresponding to the first four and the fifth cycles and have blunt dentations.

Polyps are relatively fleshy and colourful (Fig. 775).

Affinities

As noted above, this supposed species grades into *S.* cf. *vitiensis* from Lord Howe Island (Figs. 425-431). Experimental work may eventually show that all these forms are conspecific.

Distribution

Recorded only from eastern and southern Australia.

GENUS *ACANTHASTREA* EDWARDS & HAIME, 1848

Generic synonymy

Acanthastrea Edwards & Haime, 1848c; Vaughan & Wells (1943); Wells (1956); Chevalier (1975).

Type species

Acanthastrea spinosa Edwards & Haime, 1848c (= *Astrea echinata*, Dana, 1846).

Characters and affinities

Acanthastrea includes all monocentric colonial mussids which are cerioid or plocoid. It is therefore very distinct from all other mussid genera and, as noted below, is close to the faviid genera *Favites* and *Favia* in growth form, so much so that Matthai (1914) placed *Acanthastrea*, along with several other faviid genera, in the genus *Favia*. *Acanthastrea* is, however, distinct from any faviid in having mussid-like septal dentations and mussid-like polyps. The former character usually clearly distinguishes coralla of *Acanthastrea* from those of *Favites* although, as noted by Chevalier (1975), some species of *Favites* (e.g. *F. flexuosa* and *F. rotundata*) do develop large, lobed dentations, which are close to those of *Acanthastrea* species, especially *A.* cf. *bowerbanki*.

Acanthastrea echinata (Dana, 1846)

Synonymy (partly after Matthai, 1914)

Astrea dipsacea Lamarck, 1816; *non Astrea dipsacea* Audouin (1826); Edwards & Haime (1857).

Astrea echinata Dana, 1846.

Astrea patula Dana, 1846; Edward & Haime (1857).

Acanthastrea spinosa Edwards & Haime, 1848c; Edwards & Haime (1849b, 1857).

Acanthastrea hirsuta Edwards & Haime, 1857; Ma (1959).

Acanthastrea brevis Edwards & Haime, 1849b; Edwards & Haime (1857).

Acanthastrea grandis Edwards & Haime, 1849b; Edwards & Haime (1857).

Acanthastrea echinata (Dana); Edwards & Haime (1857); Whitelegge (1898); Vaughan (1918); Yabe & Sugiyama (1935c); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Crossland (1952); Wells (1954); Stephenson & Wells (1955); Ma (1959); Chevalier (1968, 1975).

Favia hirsuta (Edwards & Haime); Matthai (1914).

Favia hemprichii (Ehrenberg); Crossland (1931); *non Acanthastrea hemprichii* (Ehrenberg); Faustino (1927); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1940).

Favia dipsacea (Audouin); Crossland (1948).

Favites hirsuta (Edwards & Haime); Ma (1959).

Acanthastrea rotundoflora Chevalier, 1975.

The synonymy of the type specimens of Edwards & Haime (as proposed by Matthai, 1914) is clear as there is little difference between them. With the possible exception of *A. brevis*, which has extremely large septal dentations, all are close to various specimens in the present series. Matthai also adds *A. irregularis* Quelch. *Acanthastrea rotundoflora* is included in *A. echinata* as an ecomorph; it clearly falls within the range of variation of the present species.

Material studied

Reef 14 km NE of **Murray Islands, Murray Islands, Warrior Reef** (4 specimens), **Sue Island, Great Detached Reef, Jewell Reef** (2 specimens), **Lizard Island** (5 specimens), **Yonge Reef** (2 specimens), **MacGillivray Reef** (2 specimens), **Hope Island, Low Isles, Palm Islands** (16 specimens), **Whitsunday Islands** (5 specimens), **Parker Reef, Pompey Complex** (2 specimens), **Swain Reefs** (5 specimens), **Heron Island** (6 specimens), **Wistari Reef** (3 specimens).

These localities include collecting stations 5, 9, 17, 27, 32, 34, 35, 39, 43, 45, 55, 60, 67, 69, 74, 79, 81, 92, 97, 100, 103, 105, 110, 115, 117, 120.

Previous records from Eastern Australia

Murray Islands, Vaughan (1918), Yonge (1930a); **Low Isles,** Crossland (1952), Stephenson & Wells (1955); **Heron Island,** Stephenson & Wells (1955).

Characters

Acanthastrea echinata occurs in a wide range of biotopes, over which it shows an enormous range of variation (Figs. 432-437). It is, however, seldom abundant in any biotope and thus its range of variability has been primarily determined from a heterogeneous collection rather than from a series of intra-biotope studies. This range includes several ecomorphs which are sufficiently different from each other to permit only a very broad description of the species as a whole.

Coralla are massive, either rounded or flattened. Corallites are cerioid or plocoid, usually circular in outline and usually vary greatly in size within the one corallum. Septa are characteristically mussid, with large, lobate or echinulate dentations and smooth, or only very finely granulated, sides.

Living colonies have a thick coenosarc which is usually folded into concentric rings which join the septo-costae dentations (Figs. 776, 777). There are no consistent colour patterns. Colonies are most commonly uniform dull colours but the stomodaea surrounding oral disc and coenosarc may each be of quite different colour.

Skeletal variations

Acanthastrea echinata ecomorph rotundoflora (Figs. 436, 437).

Acanthastrea rotundoflora was described from a single specimen which Chevalier hesitantly placed in *Acanthastrea* (discussed below). This form is well represented in the present series where it appears to be largely restricted to protected bays and lagoons associated with high islands. However, as with other ecomorphs of *A. echinata*, correlations between corallite structure and environmental conditions are unclear and certainly different from those observed in most species of Faviidae.

Coralla are plocoid. Corallites vary greatly in size from 11 to 27 mm diameter. Smaller corallites bud more from the coenosarc between adjacent corallites than from the walls of the parent corallites. Septa are very regularly spaced and vary in number (12-50) according to the size of the corallites. They are not arranged in orders and, except for those which anastamose, almost all reach the columellae. They are very strongly dentate, the dentation being lobate or echinulate on the upper margins and strongly echinulate and directed towards the columellae on the lower margins. Septo-costae of adjacent corallites are regularly adjoined. Septo-costae are thickened above the thecae and taper towards the corallite centres. Costae are very well developed and are usually dentate or beaded. There are no inter-costal ridges except those formed from irregular exothecal dissepiments. The columellae are characteristically mussid in being primarily composed of trabecular septal dentations. The endothecae, which lie deep within the calices so as to be hardly visible through the septa, are usually vesicular.

Acanthastrea echinata from reef biotopes (Figs. 434-435).

Specimens from most reef biotopes are cerioid or ploco-cerioid. The size of the corallites and the appearance and ornamentation of the septa are as described above except that shaded coralla tend to develop septa which are thinner, more crowded and less dentate. The columellae, which lie deep within the calices, are usually very well developed and spongy. In ploco-cerioid coralla, the thecal rim may be clearly differentiated from the coenosteum, which is usually vesicular. Budding sometimes occurs from the wall of a parent corallite but usually involves only the coenosarc. The edge zone is usually restricted to the upper margin of colonies as the epitheca usually covers all the undersurface. This edge zone is usually the site of rapid gemmation.

Acanthastrea echinata from turbid biotopes (Figs. 432, 433).

A number of coralla from the present series, all from turbid biotopes, are tentatively placed in this species. They are cerioid, more angular than circular in

Figs. 432-437 *Acanthastrea echinata* (× 2.5).

Fig. 432 From Great Palm Island, collecting station 42.
Fig. 433 From Sue Island, collecting station 17.
Fig. 434 From Lizard Island, collecting station 32.
Fig. 435 From Lizard Island.
Fig. 436 From Bullumbooroo Bay, Great Palm Island, collecting station 35.
Fig. 437 From Frigate Cay, Swain Reefs, collecting station 81.

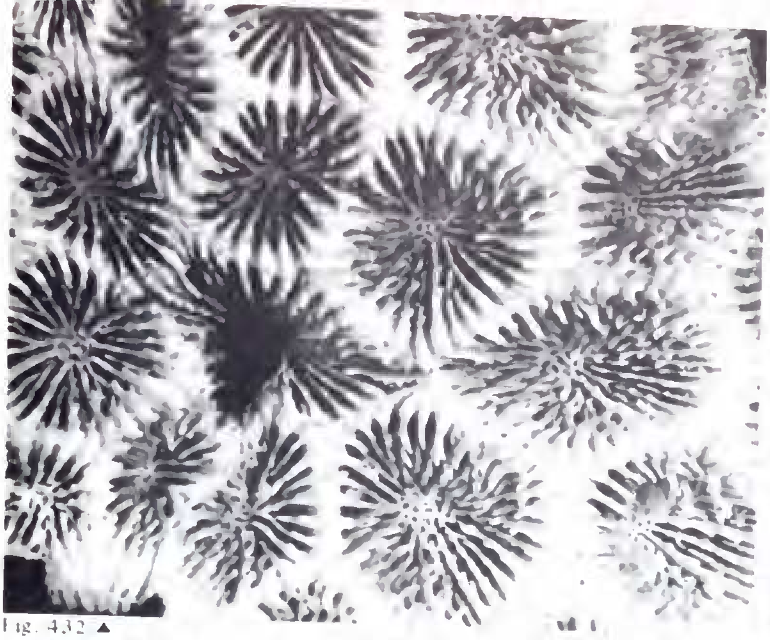


Fig. 432 ▲

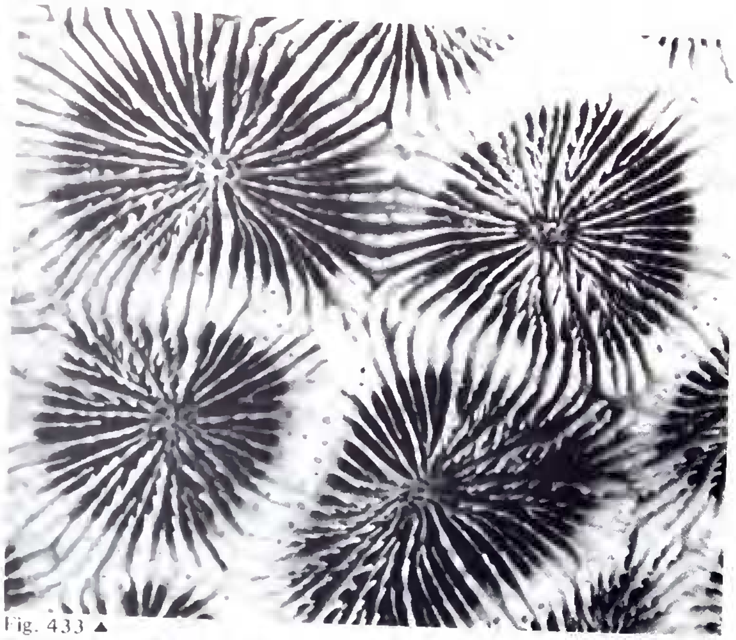


Fig. 433 ▲

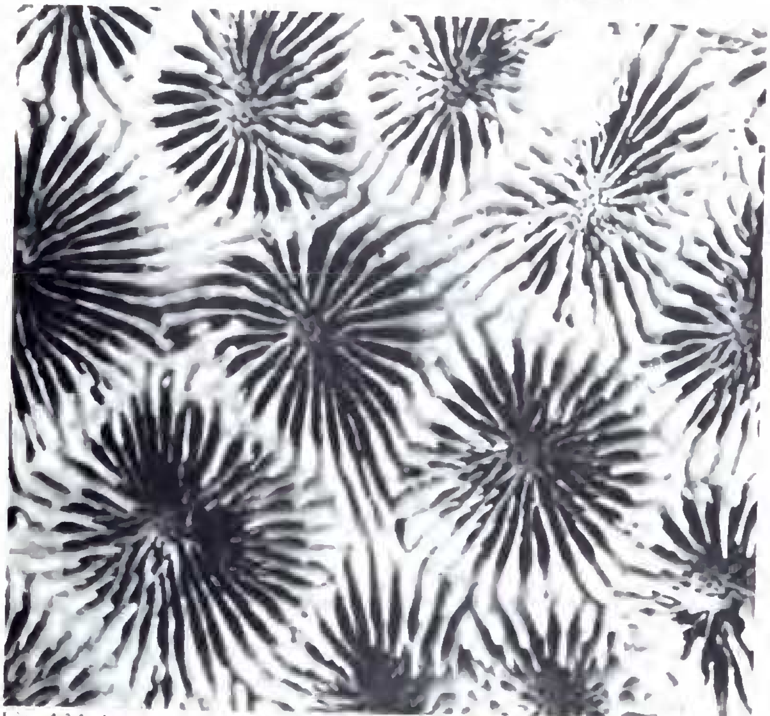


Fig. 434 ▲

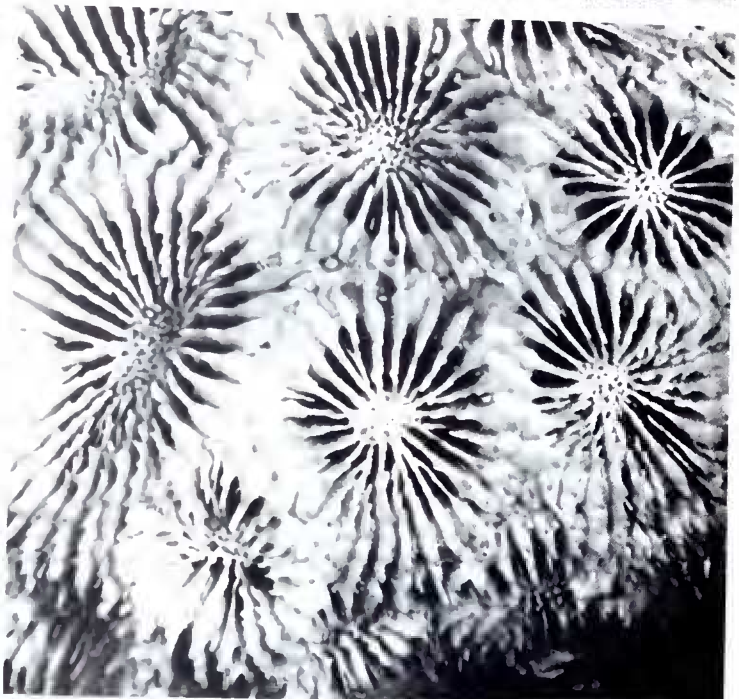


Fig. 435 ▲

Fig. 436 ▼

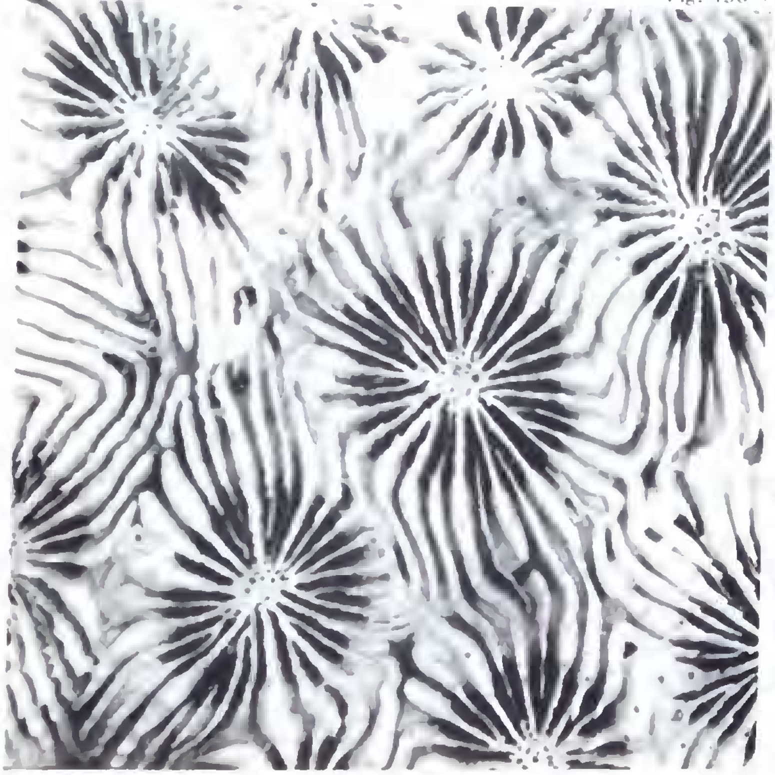
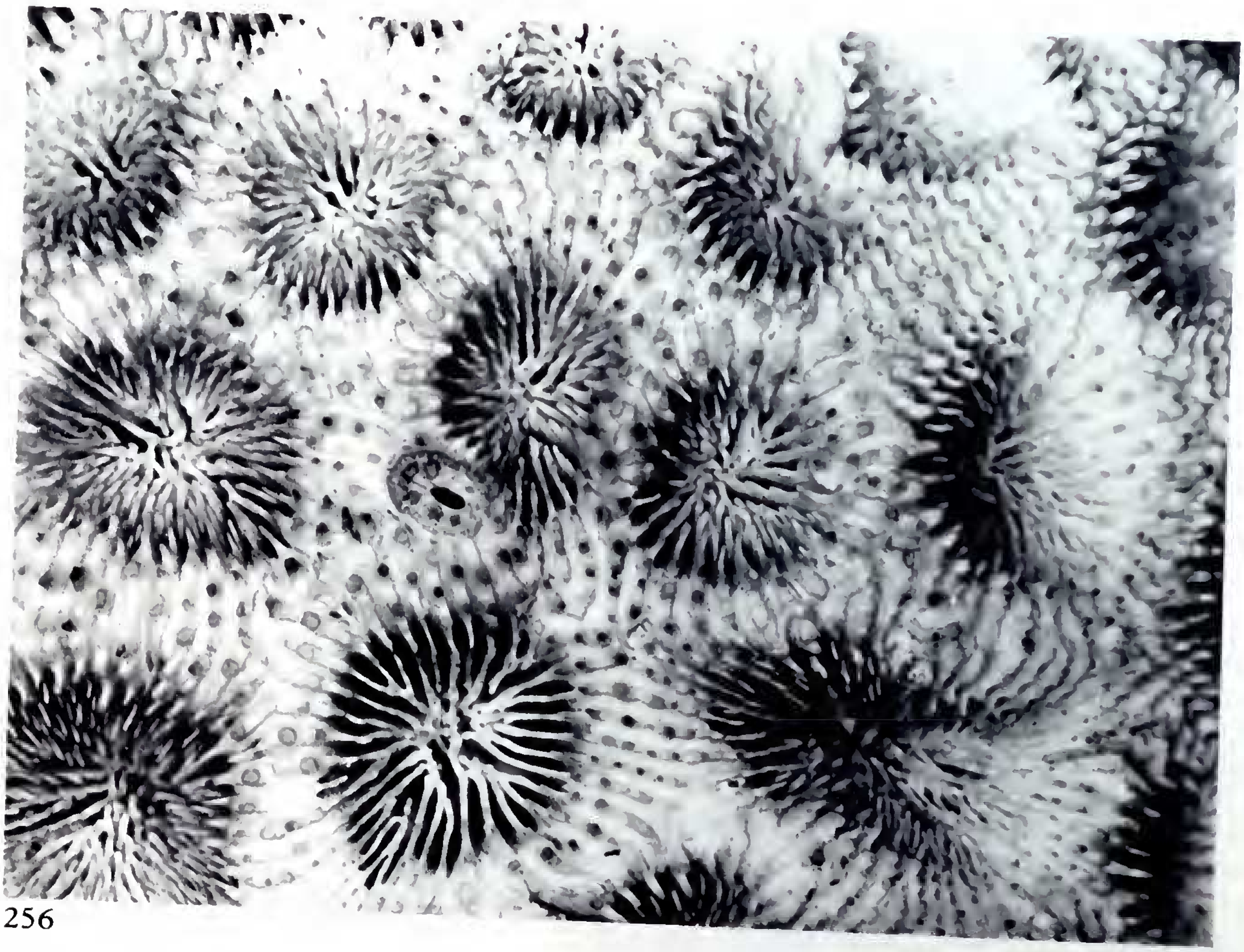


Fig. 437 ▼

Fig. 438 *Acanthastrea echinata* from the Swain Reefs, showing tentacles extended at night.

Fig. 439 Holotype of *Acanthastrea echinata.*



outline and have numerous fine septa. The septa are only slightly thickened over the theca and have up to 8 fine dentations which are nevertheless mussid in appearance. The dentations are not as exsert as they are in reefal *A. echinata.* The columellae are deep, small and compact. The common wall is relatively narrow.

This ecomorph appears to correspond to the *A. echinata* variety *pseudofavites* of Chevalier (1975).

Affinities

Chevalier (1975) separated his *A. rotundoflora* from *A. echinata* on the basis that the former is fully plocoid and shows extratentacular budding. However, extratentacular, or more particularly, coenosarc budding, is normal in all *A. echinata* and the plocoid condition appears to be common. Otherwise there is little difference between these forms as is indicated by comparing Chevalier's own figures [Plate XXXI, Fig. 5 (*A. echinata*) and Fig. 7 (*A. rotundoflora*)].

The only other species which shows close affinity with *A. echinata* is *A.* cf. *bowerbanki.* Like *A. echinata* from protected biotopes, *A.* cf. *bowerbanki* has a thin, angular, common wall. The septa, however, are far fewer and less regular and are not adjoined over the theca.

Distribution

Widely distributed from the Red Sea to the Marshall and Ellice Islands and the Tuamotu Archipelago.

Acanthastrea hillae Wells, 1955

Synonymy

? *Acanthastrea* or *Mussa* sp. Matthai, 1924.

Acanthastrea hillae Wells, 1955b; Chevalier, 1975.

Material studied

Murray Islands, Whitsunday Islands, Byron Bay, Lord Howe Island (5 specimens).

These localities include collecting stations 28, 39, 143, 147.

Previous records from Eastern Australia

Moreton Bay (subfossil) Wells (1955b); **Lord Howe Island,** Veron & Done (1979).

Characters

Coralla are usually sub-massive, with undulating surfaces of irregular shape. They may attain diameters of 1.5 m but are usually small. Most coralla are cerioid, some may be sub-plocoid. Initial growth is from a large central corallite by extratentacular budding. Daughter-corallites are usually monocentric although valleys up to 12 cm long, with up to four centres, are sometimes formed. The size and shape of corallites varies greatly. In cerioid coralla they are usually angular, 1.5-4.3 cm maximum diameter. Sub-plocoid corallites are usually 2.5 cm diameter, oval in outline and monocentric.

Septa are not clearly arranged in orders. Usually half reach the columellae. These are thicker, more exsert and more coarsely dentate than the others, the smallest of which are usually perforate and have very long, twisting inner dentations. All septa have coarsely granulated sides. The columellae are usually surrounded by an irregular circle of large dentations from the principal septa and are composed of coarse, twisted trabeculae derived from these dentations. Where valleys are formed, the columellae are adjoined by laminar linkages along the valley axis and curved septa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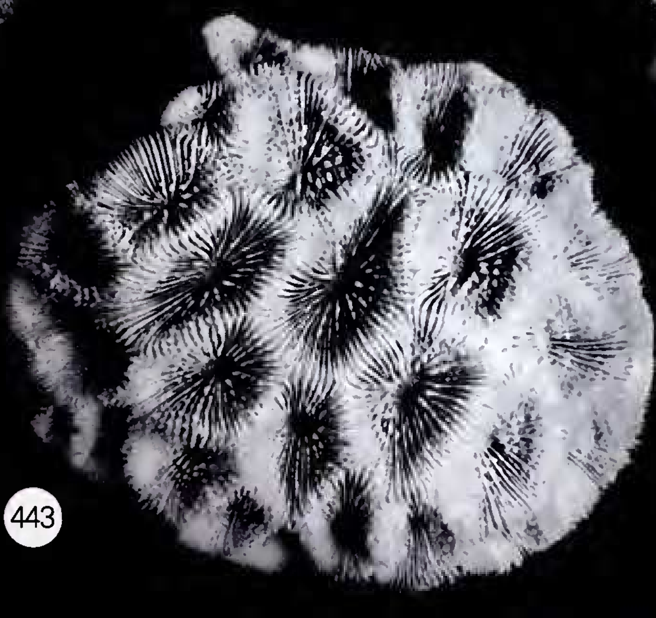
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from either side of the axis. Septa are usually equally exsert over the thecae and are usually adjoined in cerioid coralla and separated by a groove in sub-plocoid coralla.

Living coralla are very distinctive, having large fleshy polyps (Figs. 448, 779, 780) of a wide range of colours, usually red, cream and brown, in mottled patterns. Polyps are only expanded at night.

Skeletal variation

This species is very uncommon on the Great Barrier Reef. However, it is relatively abundant at Lord Howe Island where most coralla are cerioid and have relatively fine septa and elongate septal dentations. Specimens from shallow, relatively exposed biotopes are similar to Great Barrier Reef specimens, having a tendency towards a sub-plocoid form with septa greatly thickened in the vicinity of the theca.

Affinities

There is a superficial resemblance between some coralla of this species and *Moseleya latistellata* which also has a central corallite, a similar type of budding, and corallites of similar size and shape. However, coralla are distinguished by the mussid dentations of *A. hillae* and lack of paliform lobes. Living colonies are not at all similar, having polyps generally resembling other species of their respective families.

Acanthastrea hillae is perhaps closest to *A.* cf. *bowerbanki* (see below) which has corallites of similar size (Fig. 781).

Figs. 440-443 *Acanthastrea hillae* (× 0.5).

Figs. 440, 442, 443 From Lord Howe Island, collecting station 143.
Fig. 441 From Lord Howe Island, collecting station 147.

Figs. 444-447 *Acanthastrea hillae* from Lord Howe Island, same coralla as Figs. 442, 443, 441, 440 respectively (× 2.5).

Fig. 444 ▼

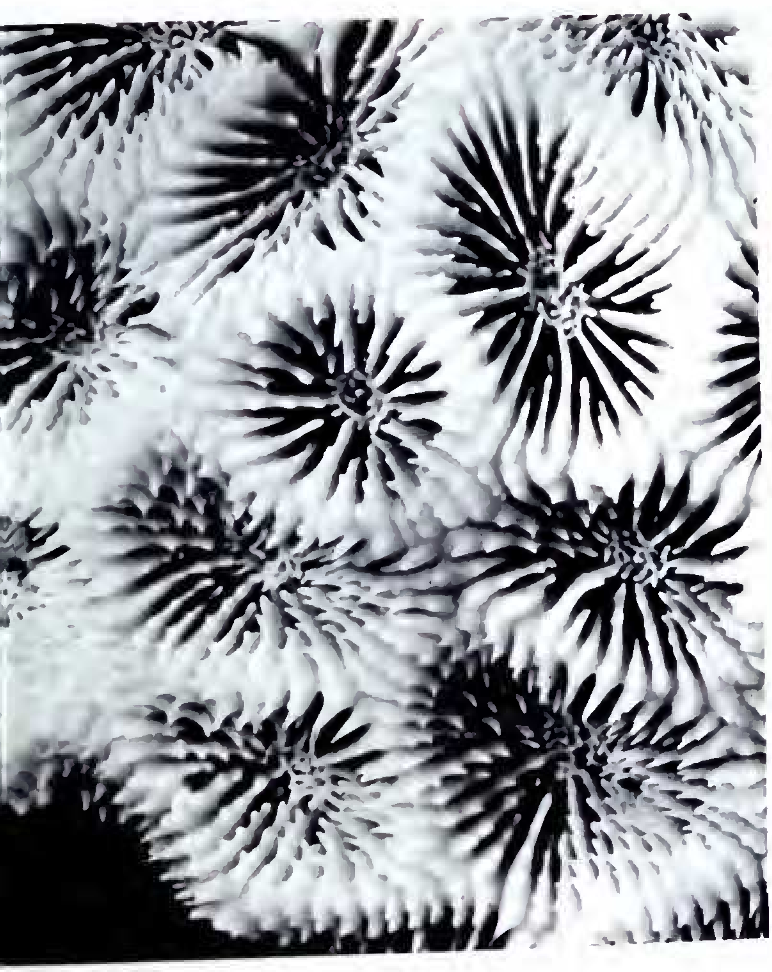


Fig. 445 ▼

Distribution

This species is previously known only from subfossils in Moreton Bay (Wells, 1955a), and a single specimen from New Caledonia (Chevalier, 1975). As previously noted, it is very rare on the Great Barrier Reef, but relatively common at Lord Howe Island where *A.* cf. *bowerbanki* is also relatively common.

Acanthastrea cf. bowerbanki Edwards & Haime, 1857

Synonymy

Acanthastrea bowerbanki Edwards & Haime, 1857.

Acanthastrea angulosa Brüggemann, 1879a.

Material studied

Heron Island, Lord Howe Island (9 specimens).
These localities include collecting stations 116, 142, 143, 145, 147.

Previous records from Eastern Australia

Lord Howe Island, Veron & Done (1979).

Characters

Colonies are submassive to encrusting, up to 1.5 m in diameter. Coralla are cerioid with irregularly shaped calices, commonly up to 2.6 cm maximum diameter. Four orders of septa may be distinguished in some coralla but these are usually irregular and frequently have anastomosed inner margins. The major septa are slightly more exsert and thicker than the others and have larger dentations. However, all septa are relatively thin and have elongate dentations of very irregular shape and size, giving the corallum a ragged appearance. They are granulated in most, but not all, coralla.

Fig. 446 ▼

Fig. 447 ▼

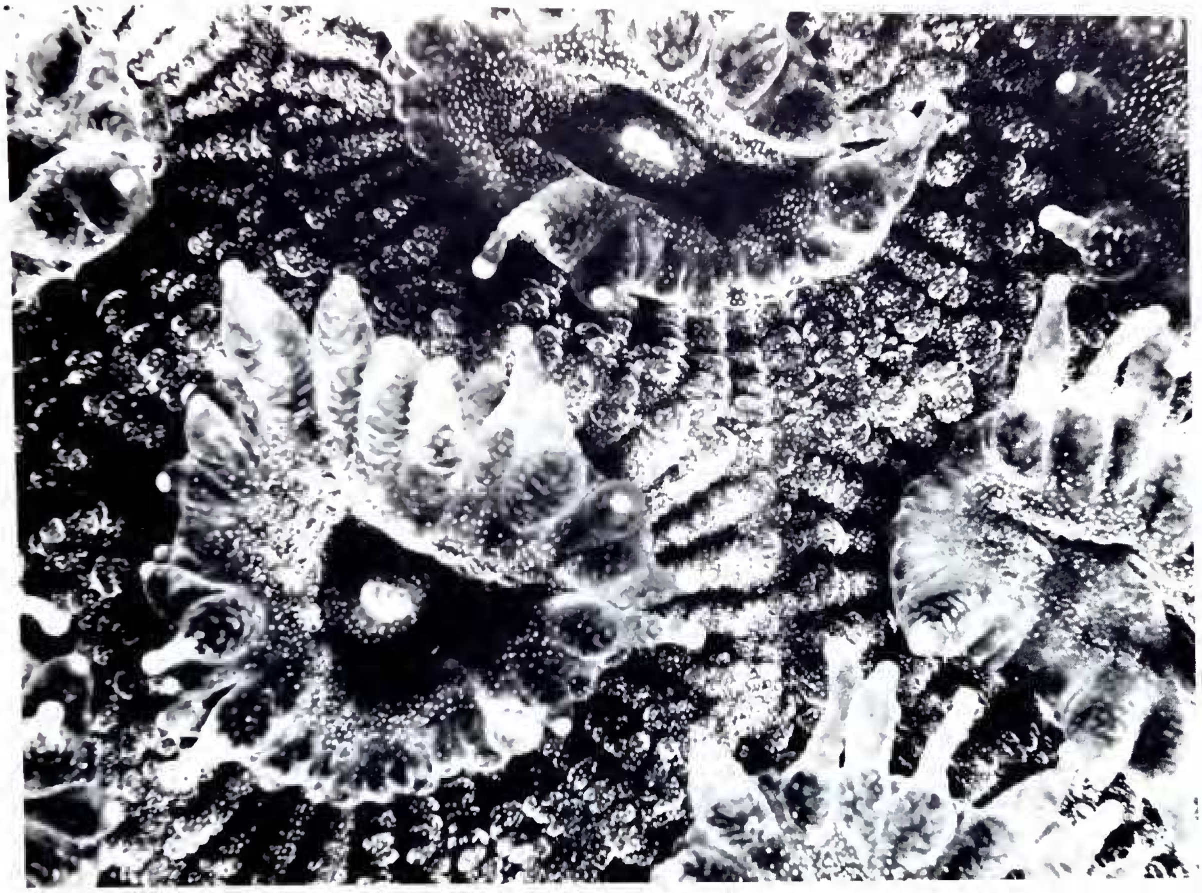


Fig. 448 *Acanthastrea hillae* from Lord Howe Island with polyps extended at night.

Figs. 449, 450 *Acanthastrea* cf. *bowerbanki* (× 0.5).

Fig. 449 From Heron Island, collecting station 116.
Fig. 450 From Lord Howe Island, collecting station 147.

The thecae are thin and irregular and the septa usually very exsert and adjoined over the thecae. In some calices, groups of septa are fused on their outer margins adjacent to the theca and all septa are thickened in the vicinity of the theca, which is primarily septothecate. The columellae are usually small and diffuse and clearly composed of twisted inner septal dentations. Budding is primarly extratentacular. In most small coralla a central calice is distinguishable, as with *A. hillae*.

Living colonies do not have the thick, fleshy polyps of other *Acanthastrea* species, rather they more closely resemble those of *Favites* (Figs. 782-784). Colonies have a wide range of colours but are most commonly pale grey or brown. Polyps are expanded only at night.

Affinities

As previously noted, living colonies more closely resemble *Favites* than other *Acanthastrea* species and thus *A.* cf. *bowerbanki* is readily distinguished from *A. hillae* underwater. Coralla of these two species are similar in their growth form and mode of budding and the range of size of the calices overlaps. They differ markedly in the appearance of the theca which is much thinner in *A.* cf. *bowerbanki* and in many characters of the septa and columellae. The latter species has thinner, more numerous septa, which are often anastomosed at either end. Septal dentations are much finer and irregular and the columellae are smaller and more diffuse.

Figs. 451-453 *Acanthastrea* cf. *bowerbanki* (× 2.5).

Figs. 451, 452 From Lord Howe and Heron Islands, same coralla as Figs. 449, 450 respectively.
Fig. 453 From Lord Howe Island, collecting station 147.

Fig. 451 ▼

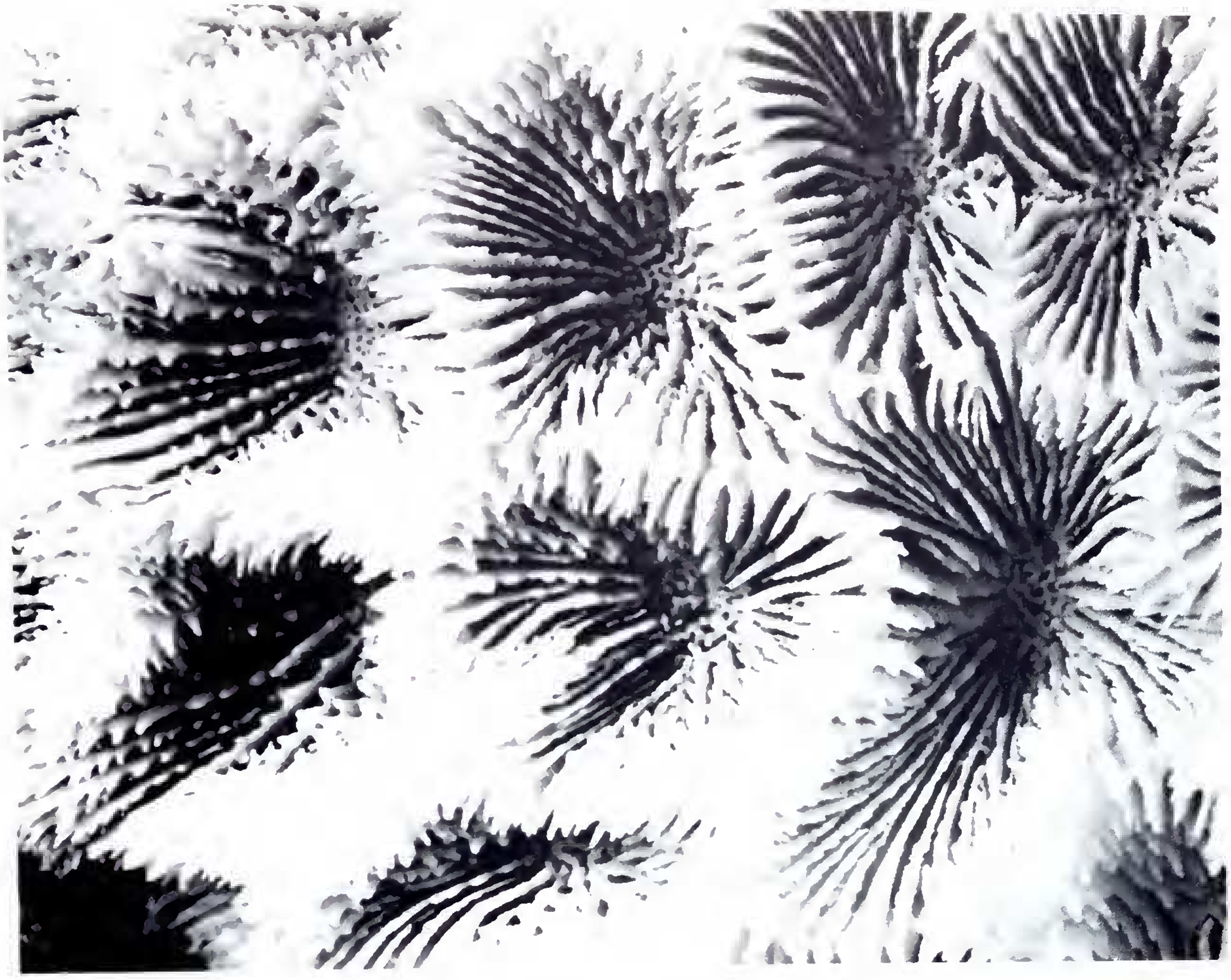
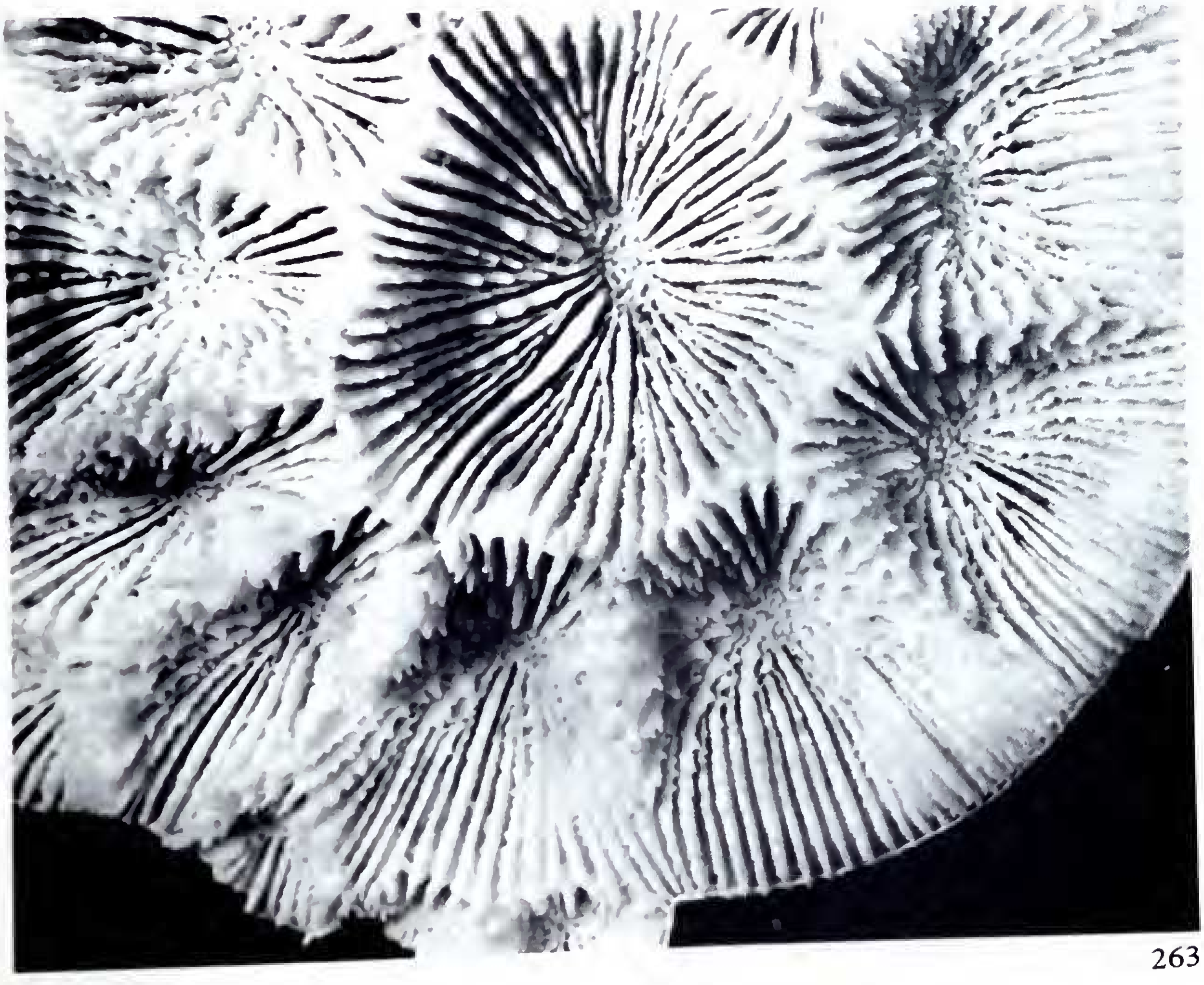


Fig. 452 ▲

Fig. 453 ▼



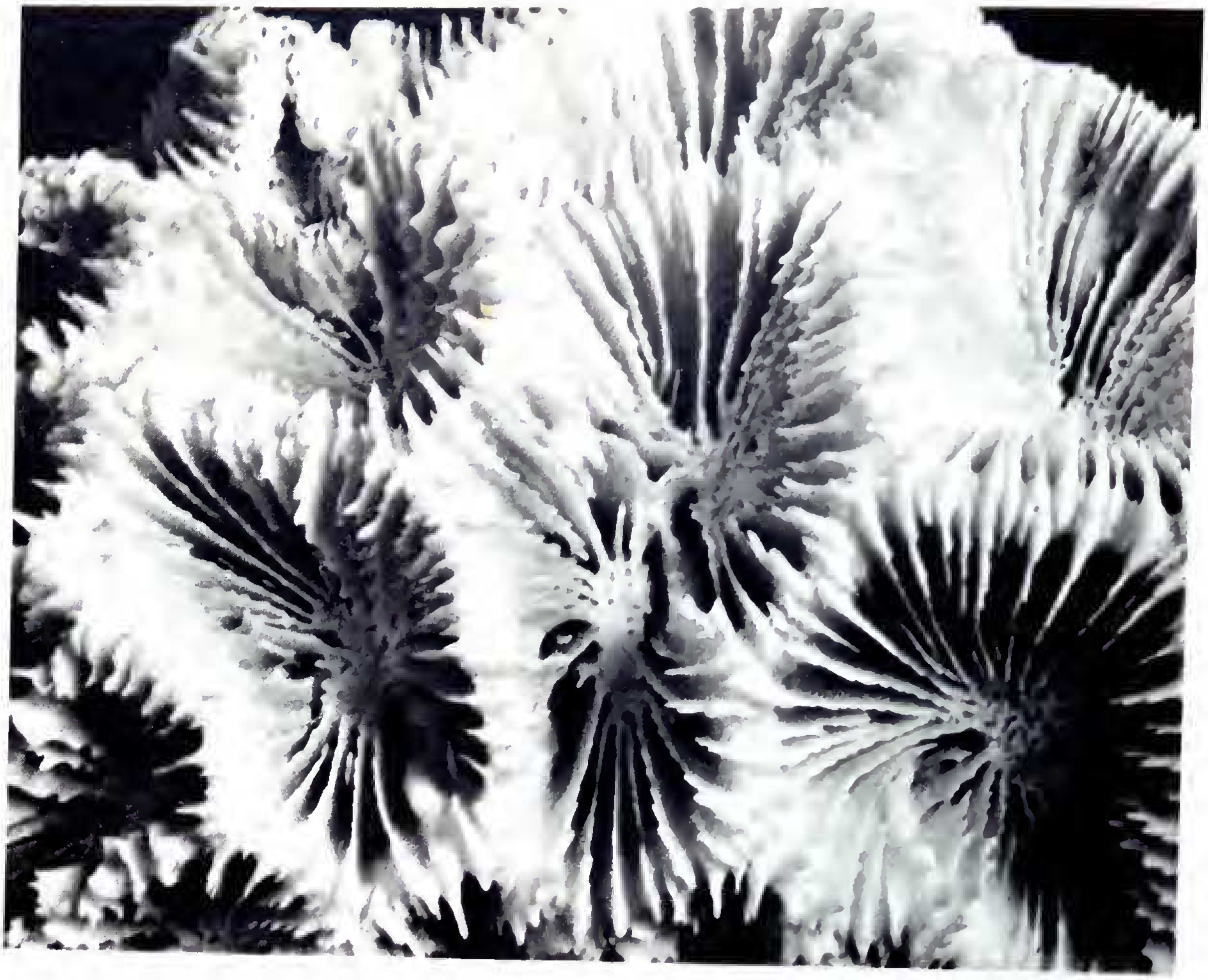


Fig. 454 Holotype of *Acanthastrea* cf. *bowerbanki* (× 1.0).

Distribution

As with *A. hillae* this species is rare on the Great Barrier Reef but relatively abundant at Lord Howe Island. Previous records are only of the holotype from 'Australia' and the holotype of *A. angulosa* from the island of Rodriguez in the western Indian Ocean.

Acanthastrea sp.

Material studied

Lord Howe Island, principal collecting station 142.

Previous records from Eastern Australia

Lord Howe Island, Veron & Done (1979).

Characters

A single colony of this very distinct species of *Acanthastrea* was found in North Bay, Lord Howe Island, at 2 m depth. The corallum is massive, dome shaped, approximately 20 cm across, and very dense. It is cerioid with calices up to 2 cm maximum dimension. Calices are deep, polygonal in shape, with angular thecae giving a cellular appearance. Thecae are thin, with vertical sides. Septa are very irregular. They are short and thick and usually consist of little more than ridges

Figs. 455, 456 *Acanthastrea* sp., same corallum from Lord Howe Island (× 0.5 and 2.5 respectively).

Fig. 455 ▲

Fig. 456 ▼

extending down the upper half of the thecae. Their inner margins support very large, very irregular, dentations. The columellae are absent or consist of a diffuse tangle of elongate septal dentations. Budding occurs on the upper margins of the collines.

This specimen had large grey polyps expanded approximately 2 cm during the day. They were very slow to retract.

Affinities

This specimen shows no resemblance to any other east Australian *Acanthastrea* nor to any other described species of extant corals. No other specimen of this species was seen at Lord Howe Island during a detailed study of the island corals. These observations suggest that the present specimen is either some form of gross abnormality of some other *Acanthastrea* species, or else is a relict of a nearly extinct species.

GENUS *LOBOPHYLLIA* DE BLAINVILLE, 1830

Generic synonymy

Lobophyllia de Blainville, 1830; Matthai (1928); Vaughan & Wells (1943); Wells (1956); Chevalier (1975).

Type species *Madrepora corymbosa* Forskål, 1775.

Characters of the genus

Coralla are phaceloid to flabellate, formed by intratentacular budding. Centres have lamellar linkages and are mostly laterally free.

Introduction

Three nominal species of *Lobophyllia* have been recognised by most recent authors: *L. hemprichii*, *L. costata* and *L. corymbosa* and only three others, *L. pachysepta*, *L. hataii* and *L. robusta* have been recognised by any author since Ma (1959). With the possible exception of the last, all of these forms occur on the Great Barrier Reef where they are divisible into one very common, polymorphic species, *L. hemprichii* (with many synonyms including *L. costata*) and three less common, less variable species, *L. corymbosa*, *L. pachysepta* and *L. hataii.*

Lobophyllia hemprichii (Ehrenberg, 1834)

Synonymy (partly after Matthai, 1928 and Chevalier, 1975)

Manicina hemprichii Ehrenberg, 1834.

Madrepora cristata Esper, 1789; *non* Ellis & Solander (1786).

Caryophyllia cristata (Esper); Ehrenberg (1832).

Mussa costata Dana, 1846; Edwards & Haime (1857); Whitelegge (1898); Gardiner (1899a).

Mussa sinuosa (Lamarck); (*pars*) Dana (1846); Ortmann (1888); Gardiner (1899a); Vaughan (1918); Matthai (1923a); Hoffmeister (1925); Faustino (1927); Yabe & Sugiyama (1932b).

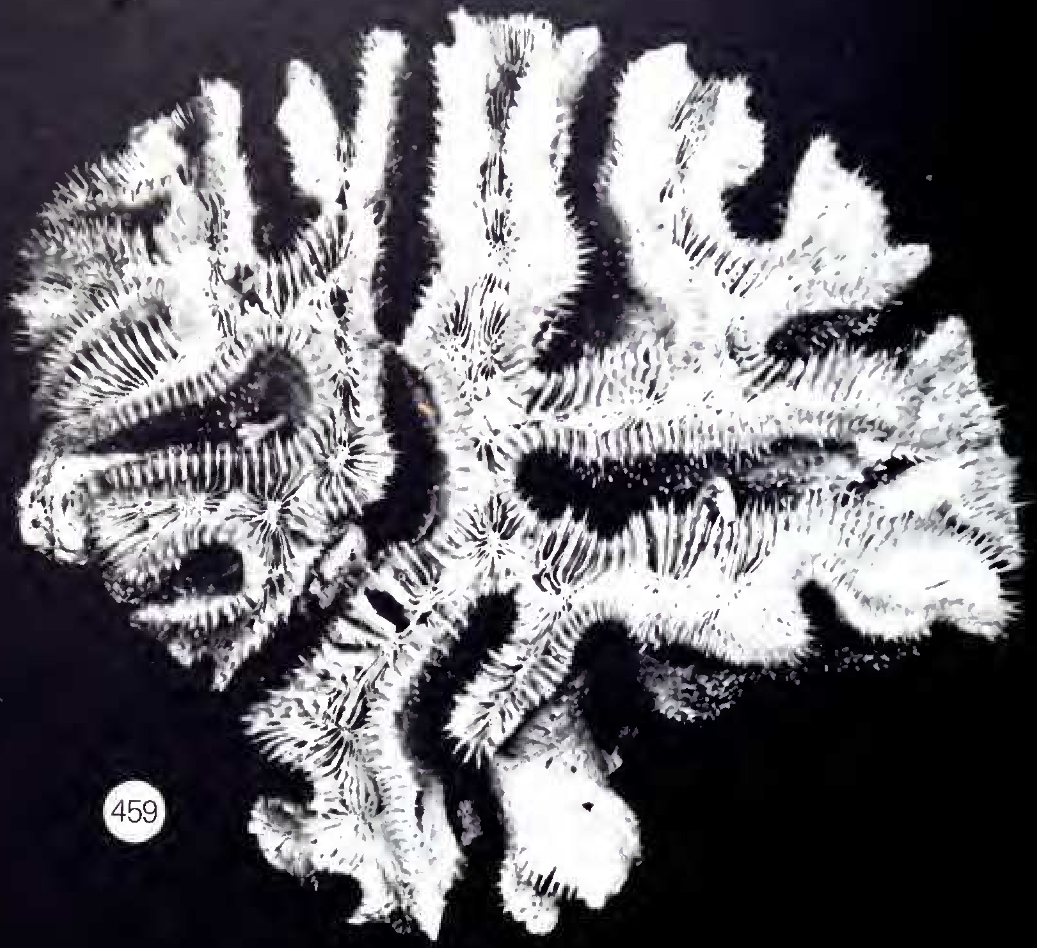
Mussa cytherea Dana, 1846; Edwards & Haime (1857); Verrill (1864).

Figs. 457-460 *Lobophyllia hemprichii*, Figs. 458-460 (× 0.5).

Fig. 457 From Turtle Backed Island, collecting station 138 (× 0.3).
Fig. 458 From Wyer Island, Murray Islands, collecting station 30.
Figs. 459, 460 From Wistari Reef.

457

458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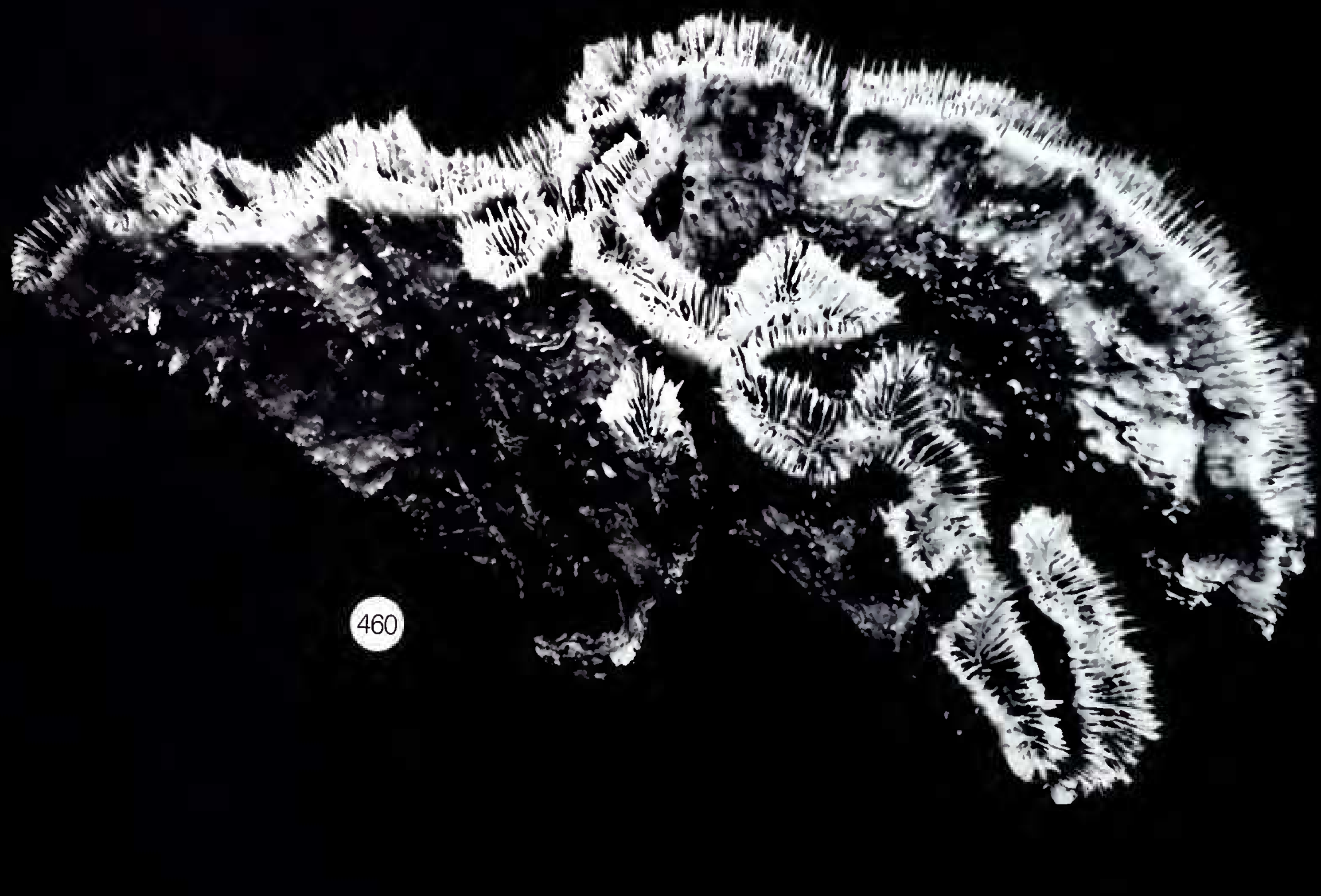
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Mussa multilobata Dana, 1846; Edwards & Haime (1857); Quelch (1886); Gardiner (1899a); Faustino (1927).

Lobophyllia aspera Edwards & Haime, 1849a.

Lobophyllia tenuidentata Edwards & Haime, 1849a.

Lobophyllia cristata (Esper); Edwards & Haime, 1849a.

Lobophyllia flexuosa Edwards & Haime, 1849a.

Lobophyllia echinata Edwards & Haime, 1849a.

Lobophyllia sinensis Edwards & Haime, 1849a.

Mussa aspera (Edwards & Haime); Edwards & Haime (1857); Quelch (1886); Ortmann (1888).

Mussa tenuidentata (Edwards & Haime); Edwards & Haime (1857); Verrill (1864); Studer (1881); (as *M. tenuidentina*) Yabe & Sugiyama (1932).

Mussa cristata (Edwards & Haime); Edwards & Haime (1857); Klunzinger (1879); Rehberg (1892); Gardiner (1899a); Harrison & Poole (1909b); Gravier (1911); Faustino (1927).

Mussa flexuosa (Edwards & Haime); Edwards & Haime (1857).

Mussa echinata (Edwards & Haime); Edwards & Haime (1857); Quelch (1886); Bedot (1907); Matthai (1924).

Mussa sinensis (Edwards & Haime); Edwards & Haime (1857).

Mussa hemprichii (Ehrenberg); Edwards & Haime (1857); Klunzinger (1879); Rehberg (1892); Gardiner (1899a); Gravier (1911).

Mussa solida Tenison-Woods, 1879b.

Mussa distans Klunzinger, 1879.

Mussa erythraea Klunzinger, 1879; Gravier (1911).

Mussa brueggemanni Quelch, 1886; Bedot (1907); Matthai (1924).

Mussa studeri von Marenzeller, 1901.

Lobophyllia hemprichii (Ehrenberg); Matthai (1928); Crossland (1931, 1935, 1952); Thiel (1932a); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Ma (1937, 1959); Eguchi (1938); Wells (1954); Stephenson & Wells (1955); Searle (1956); Nemenzo (1959); Pichon (1964); Scheer (1967); Pillai, Vine & Scheer (1973); Chevalier (1975).

Lobophyllia costata (Dana); Matthai (1928); Crossland (1931, 1935, 1938); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Ma (1937, 1959); Eguchi (1938); Umbgrove (1940); Wells (1954); Rossi (1954); Stephenson & Wells (1955); Scheer (1967); Chevalier (1968, 1975); Rosen (1971).

The above synonymy is largely based on opinions expressed by earlier authors and the junior synonyms of species they considered valid. Much of it is of historical interest only, and results from the combining of *L. hemprichii* and *L. costata*, considered distinct by previous authors. Chevalier (1975), among others, has expressed uncertainty in maintaining both names and clearly there is little evidence from skeletal studies of heterogeneous collections for either separation or combination. This question can only be resolved by underwater observation and consequent study of intra-biotope variation.

This was undertaken during the present study within many biotopes at Heron Island, the Palm Islands and the Whitsunday Islands where *Lobophyllia* are abundant. No basis was found for dividing the present group which, consequently, appears to be a single, widespread, very polymorphic species.

Material studied

Campbell Island (2 specimens), **Big Mary Reef** (3 specimens), **Yorke Island** (4 specimens), **Dungeness Reef** (5 specimens), **Turtle Backed Island, Murray Islands** (3 specimens), barrier reef E of **Murray Islands** (2 specimens), **Thursday Island, Great Detached Reef** (10 specimens), **Tijou Reef** (4 specimens), **Bewick Island** (3 specimens), **Jewell Reef** (4 specimens), **Lizard Island** (4 specimens), **Hope Island** (14 specimens), **Low Isles** (7 specimens), **Palm Islands** (95 specimens), **Magnetic Island, Old Reef** (19 specimens), **Gould Reef** (2 specimens), **Bait Reef** (4 specimens), **Whitsunday Islands** (19 specimens), **Bushy Island-Redbill Reef** (5 specimens), **Parker Reef** (2 specimens), **Swain Reefs** (7 specimens), **Heron Island** (30 specimens).

These localities include collecting stations 1, 2, 5, 13, 18, 26, 28, 30, 32, 34, 35, 36, 37, 38, 41, 42, 43, 45, 54, 55, 57, 59, 60, 69, 73, 79, 80, 81, 91, 96, 97, 98, 100, 102, 117, 122, 123, 125, 126, 131, 132, 138.

Previous records from Eastern Australia

Murray Islands (as *L. costata*) Vaughan (1918); **Low Isles**, Crossland (1952), (as *L. hemprichii* and *L. costata*) Stephenson & Wells (1955).

Characters

Coralla are flat to hemispherical and are frequently several metres in diameter. They may be monocentric to highly meandroid or various mixtures of both. In the latter case, elongate valleys form where space is not limiting and short valleys form in enclosed areas. Thus, variation in the meanderisation index

$$I_m = \frac{\text{number of centres,}}{\text{number of valleys}}$$

one of the primary sources of taxonomic instability in the species, is partly a function of available space and partly a function of water quality and light availability (see below).

Apart from the I_m, *L. hemprichii* shows wide variations in most calicular structures. Septa may be arranged in four distinct orders or two alternating orders or orders may be indistinguishable. First order septa are highly exsert and strongly dentate. The shape of the dentations varies from lobate to echinulate and their number usually varies from 2-10. The dentations are seldom uniform along the length of the septal margin; in some coralla they become more lobate towards the columella. Septa of higher orders have finer, more numerous dentations. All septa have finely serrated margins and finely granulated sides. Those of the first order reach the columella; those of higher orders usually have free inner margins except in small corallites. The columellae are usually trabecular. The endotheca is vesicular and usually very fine. Costae are always distinguished although they usually consist of little more than parallel ridges supporting rows of sharp dentations.

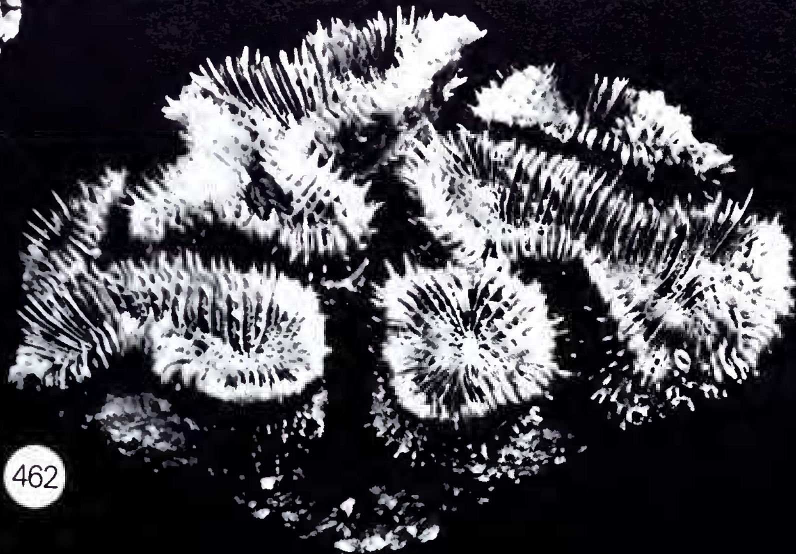
Skeletal variation

There is little variation in the fine structure of calices from within individual coralla and usually this is true of large colonies from the same biotope. The reverse usually applies to growth form variation. Individual coralla may be uniformly

Figs. 461-465 *Lobophyllia hemprichii* (× 0.5).

Fig. 461 From the Swain Reefs, collecting station 79.
Fig. 462 From Jewell Reef, collecting station 61.
Fig. 463 From Hope Island.
Fig. 464 From Bullumbooroo Bay, Great Palm Island.
Fig. 465 From Happy Bay, Long Island, Whitsunday Islands, collecting station 102.

461



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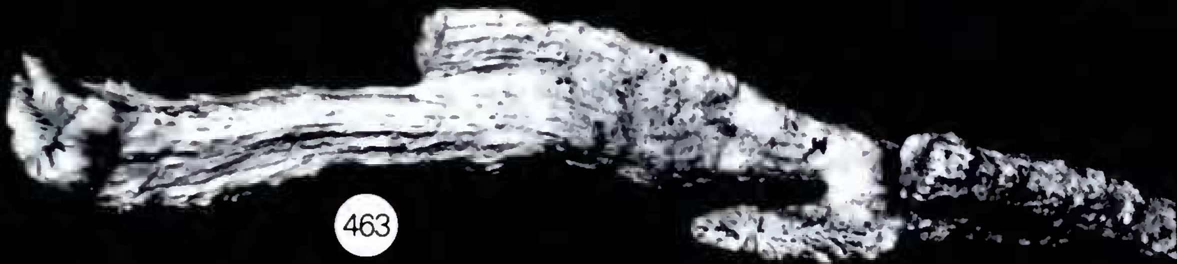

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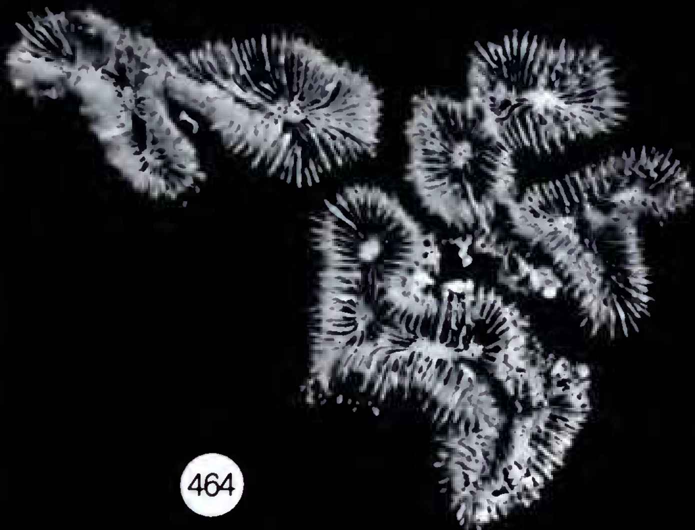

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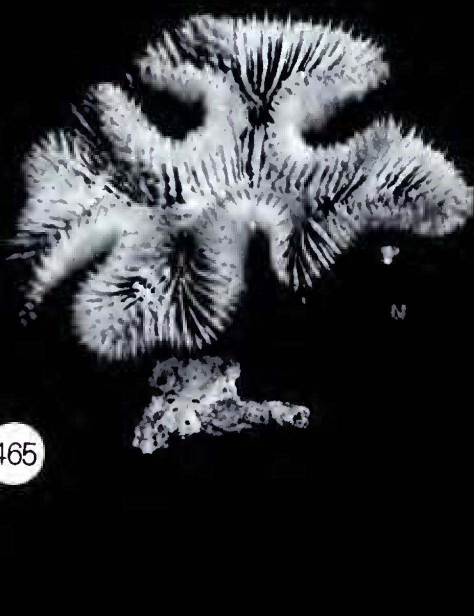


465


Fig. 466 ▲


Fig. 467 ▲

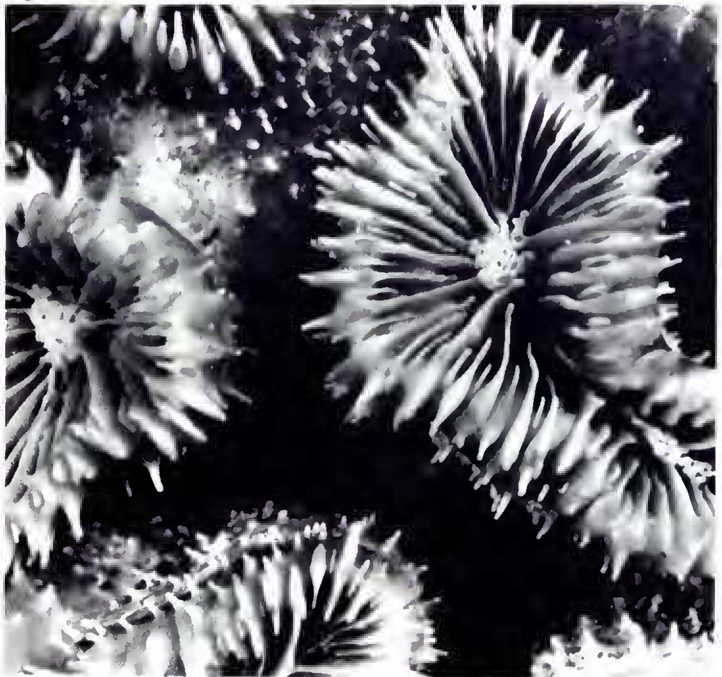


Fig. 468 ▲


Fig. 469 ▲

Fig. 470 ▼

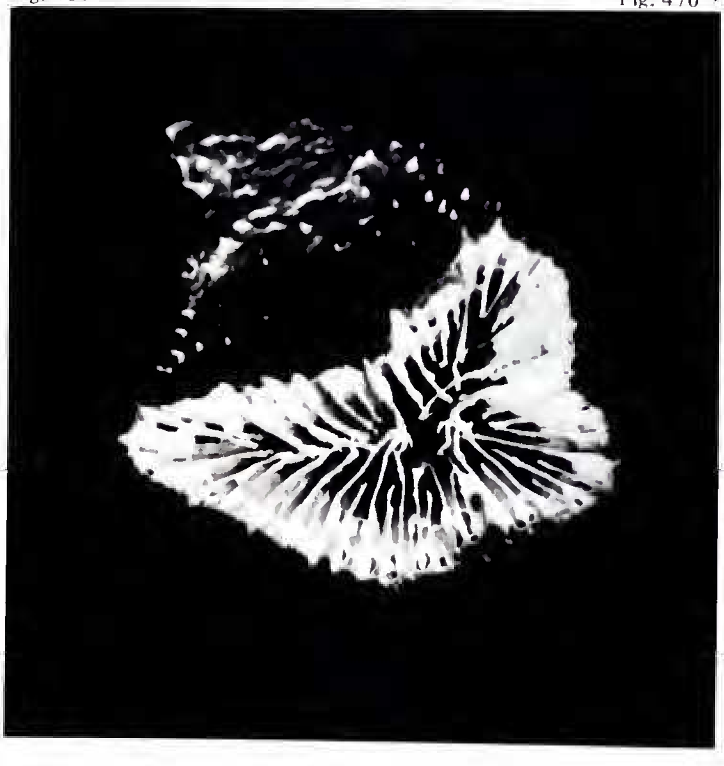


Fig. 471 ▼

monocentric; others from the same biotope may be highly flabellate, others may be various combinations of both. Frequently, the full range of growth form variation observed within a single biotope is found within individual colonies. Conversely, nearby colonies may show very little variation.

Figures 459, 460, 785-790 are of *L. hemprichii* from a single biotope at Wistari Reef where this species is extremely abundant. Some coralla are phaceloid, monocentric or nearly so, with mean corallite diameters of 3.5 cm. These may have short (3 cm) to very elongate (25 cm) branches, the latter being restricted to large colonies where the growing surface is limited. Some coralla are flabellate, sometimes with long, linear series (Fig. 460), sometimes with frequently branching series (Fig. 459). In the latter case valleys tend to be arranged radially with lateral growth occurring at the colony perimeter.

Much of the growth form variation of *L. hemprichii* appears to result from competition for space between individual branches of the same colony or branches of adjacent colonies in close proximity. Large hemispherical colonies with an even growth surface tend to be phaceloid. If the growth surface is uneven one individual corallite may outgrow one or more adjacent corallites and smother them. The free space then made available may induce that corallite to commence a (usually temporary) flabellate growth form.

The I_m of individual colonies is maximal where valleys are arranged in rows or where they radiate, but is usually reduced, again because of space limitations, in colonies where valleys grow at irregular angles. In cases where growing valleys converge, one or both valleys change their direction of growth or cease lateral expansion. In colonies with irregular surfaces, one valley may grow over the top of an adjacent converging valley, but adjacent valleys never anastomose and seldom grow closer than 1 cm.

Polyp variation

Underwater recognition of *L. hemprichii* is made difficult by the extremely varied appearance of living polyps of different colonies (Figs. 785-790). Little variation occurs in polyps of the same colony, and most of what does occur is clearly attributable to varying stages of polyp extension. Many colonies in close proximity may also have essentially identical polyps, but it is clear that in most cases these colonies have grown from dislodged parts of the same parent colony (apparently a common means of reproduction in this species). Colonies of different genotypes have polyps which vary widely in colour and morphology. Usually there are three concentric zones of each polyp which may be differently coloured: the central oral disc, the inner valley or corallite wall, and the outer wall down to the edge zone. Each of these zones may be almost any colour but frequently they are all the same colour. The ectoderm of some colonies may be mostly smooth with the septal dentations hardly visible, in others the ectoderm adheres closely to the dentations and consequently has a spiny appearance, in others the ectoderm has a rough appearance due to the growth of tubercles of variable shapes and dimensions.

It is common for colonies growing in the same biotope to have various ectodermal morphologies associated with specific colour patterns. It is also common to find polymorphic 'colonies' which have the shape of a single colony but which are composed of several colonies growing as one (Figs. 788-790). However, no correla-

Figs. 466-471 *Lobophyllia hemprichii* (× 2.0).

Figs. 466, 467 From Wistari Reef, same coralla as Figs. 459, 460 respectively.
Fig. 468 From the Swain Reefs, same corallum as Fig. 461.
Fig. 469 From Jewell Reef, same corallum as Fig. 462.
Fig. 470 From Hope Island, same corallum as Fig. 463.
Fig. 471 From Bullumbooroo Bay, Great Palm Island, same corallum as Fig. 464.

tions have been found between skeletal variation and polyp variation; it appears that the former is largely phenotypic, the latter almost entirely genotypic.

Affinities

Matthai (1928) gave many of the earlier synonyms of *costata* and *hemprichii* and established the usage of the genus *Lobophyllia*. In 1931 Crossland combined these two species with *L. corymbosa* and thereafter these names have been confused. *Lobophyllia corymbosa* is initially distinguished from *L. hemprichii* by its mono- to tricentric corallites. It is distinguished from monocentric *L. hemprichii* by having smaller corallites with relatively regular primary septa, regular, lobate septal dentations and better developed costae. Coralla from similar biotopes are markedly different, with *L. hemprichii* always having markedly more meandroid and markedly larger corallites. *Lobophyllia hemprichii* may also have some characters in common with *L. hataii* (see p. 281 below).

Distribution

Common and widely distributed from the Red Sea to Tonga, Tahiti and the Tuamotu Archipelago.

Lobophyllia corymbosa (Forskål, 1775)

Synonymy (partly after Matthai, 1928)

Madrepora corymbosa Forskål, 1775; Quoy & Gaimard (1824).

Mussa corymbosa Dana 1846; Edwards & Haime (1857); Klunzinger (1879); Bourne (1888); Rehberg (1892); Gardiner (1904); von Marenzeller (1907); Matthai (1924, 1926).

Mussa cactus Dana 1846; Edwards & Haime (1857); Gardiner (1899a).

Lobophyllia rudis Edwards & Haime 1849a; Edwards & Haime (1857); Ortmann (1888).

Lobophyllia eydouxi Edwards & Haime, 1849a.

Lobophyllia ringens Edwards & Haime, 1849a.

Lobophyllia fistulosa Edwards & Haime, 1849a.

Lobophyllia corymbosa (Forskål); Matthai (1928); Crossland (1931, 1935, 1938, 1941, 1952); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Umbgrove (1940); Wells (1954, 1955b); Rossi (1954); Stephenson & Wells (1955); Nemenzo (1959); Ma (1959); Pichon (1964); Scheer (1967, 1972); Chevalier (1968, 1975); Rosen (1971); Pillai & Scheer (1973); Pillai, Vine & Scheer (1973); Scheer & Pillai (1975).

Mussa rudis (Edwards & Haime); Edwards & Haime (1857).

Mussa eydouxi (Edwards & Haime); Edwards & Haime (1857).

Mussa glomerata (Edwards & Haime); Edwards & Haime (1857).

Mussa ringens (Edwards & Haime); Edwards & Haime (1857).

Mussa fistulosa (Edwards & Haime); Edwards & Haime (1857).

Mussa aspera (Edwards & Haime); Edwards & Haime (1857).

Fig. 472 *Lobophyllia corymbosa* from the Palm Islands (× 0.5).

Figs. 473, 474 *Lobophyllia corymbosa* (× 2.0).

Fig. 473 From Pioneer Bay, Orpheus Island, Palm Islands, collecting station 45.
Fig. 474 From the Palm Islands, same corallum as Fig. 472.

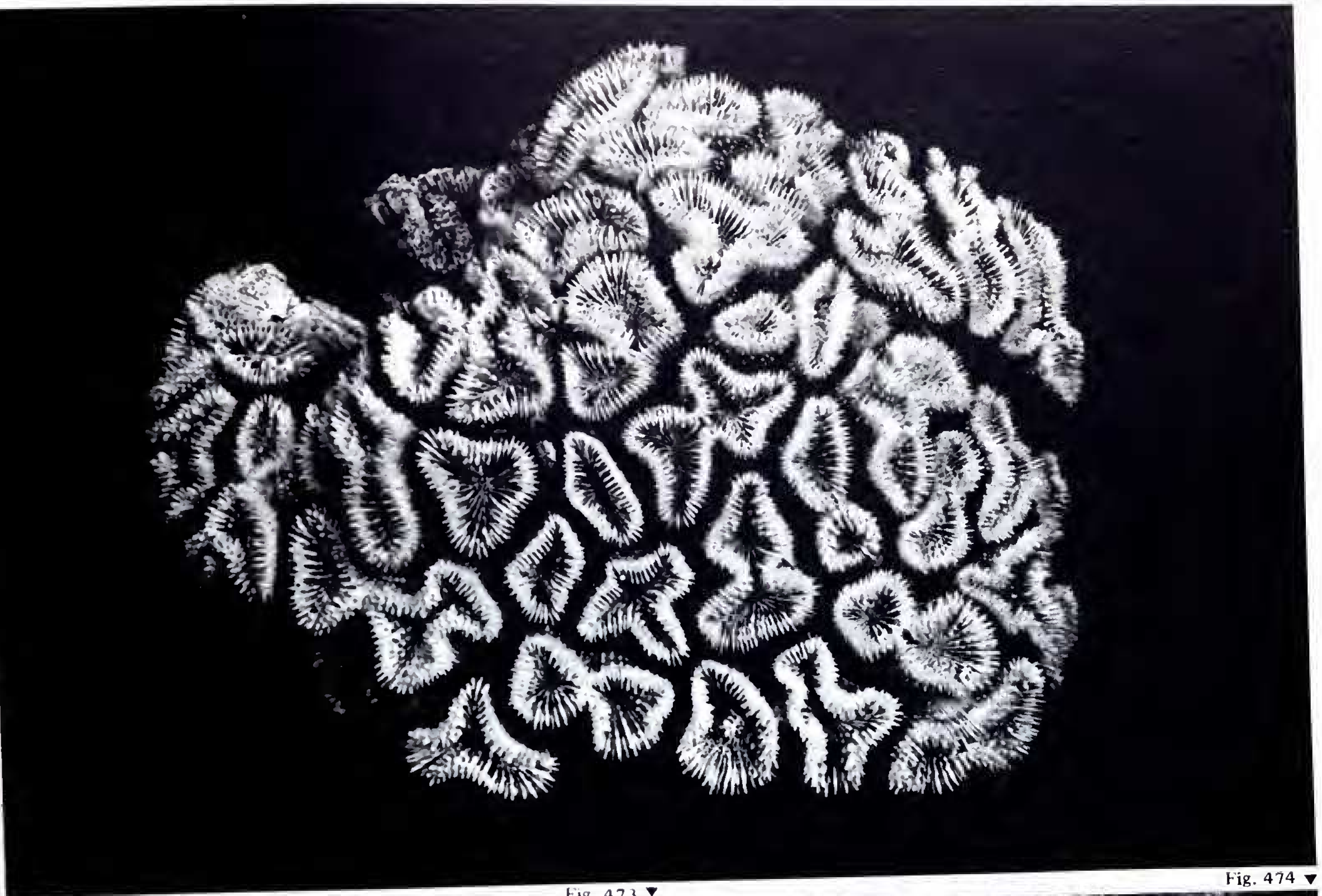


Fig. 472 ▲

Fig. 473 ▼

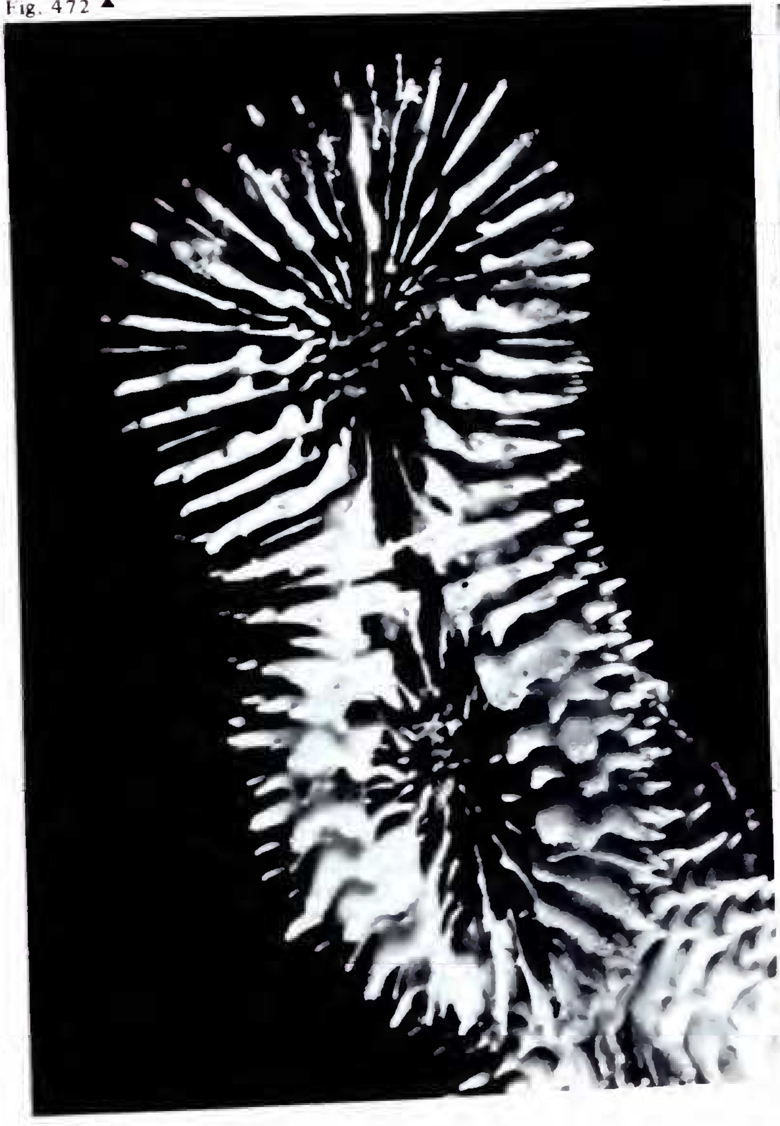
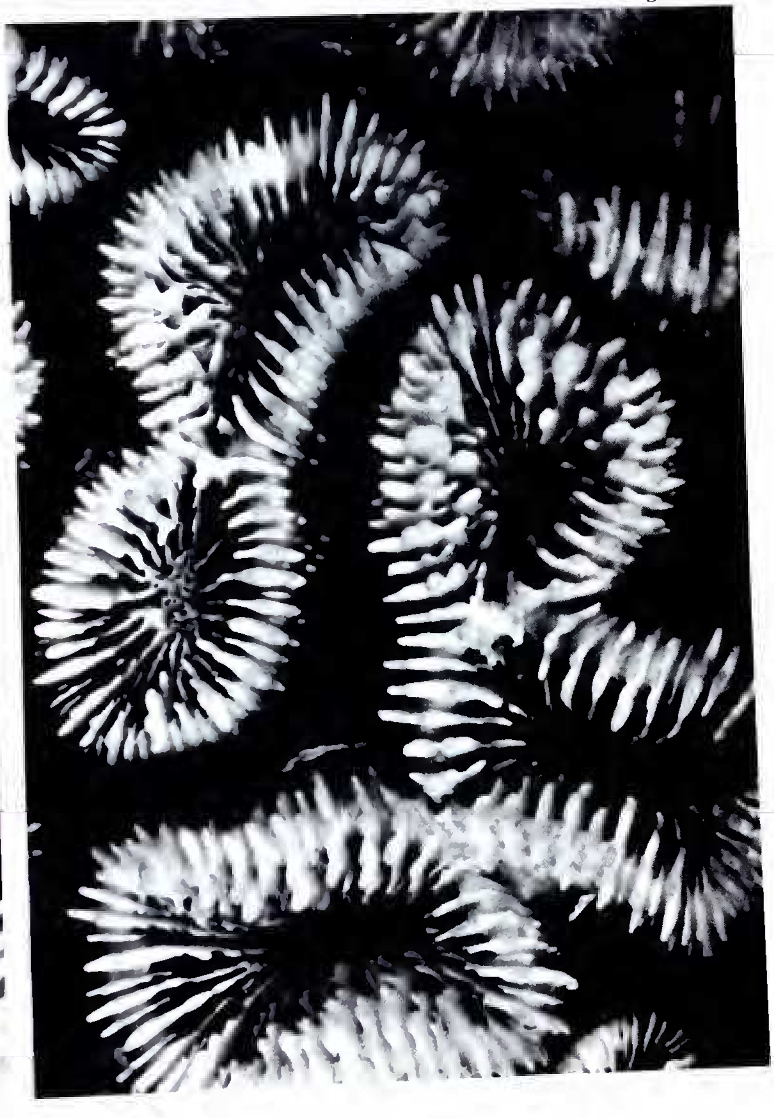


Fig. 474 ▼



Material studied

Yorke Island, Lizard Island, MacGillivray Reef, Low Isles, Palm Islands (17 specimens), **Old Reef, Whitsunday Islands** (7 specimens), **Bushy Island-Redbill Reef, Parker Reef, Pompey Complex, Swain Reefs** (5 specimens), **Heron Island** (5 specimens), **Wistari Reef.**

These localities include collecting stations 12, 34, 37, 42, 43, 45, 55, 57, 69, 74, 76, 79, 80, 81, 94, 97, 98, 100, 103, 117, 126.

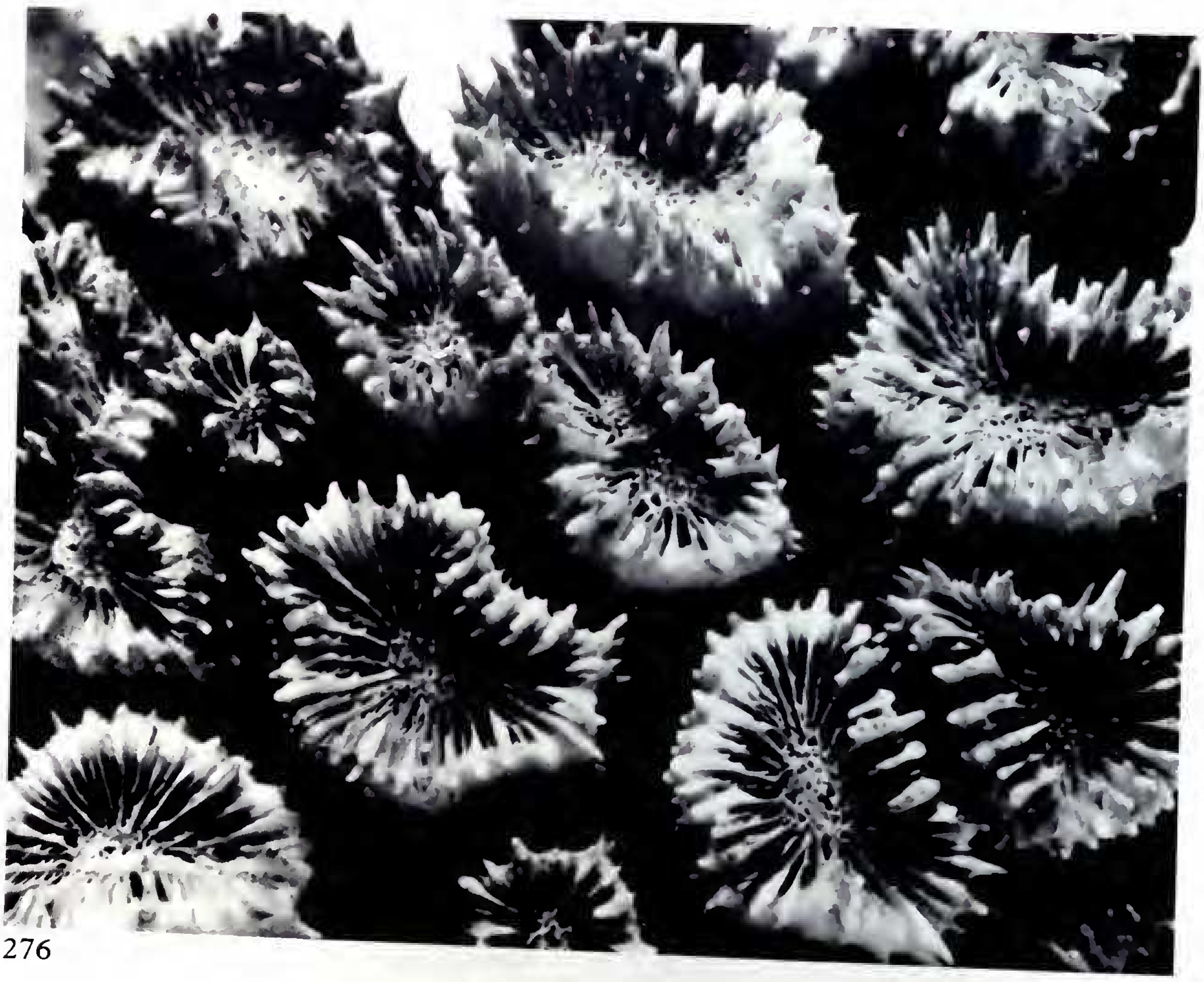
Previous records from Eastern Australia

Low Isles, Yonge (1930), Yonge & Nicholls (1930, 1931a, 1931b), Yonge *et al.* (1932), Marshall & Stephenson (1933), Stephenson & Stephenson (1933), Manton (1935), Crossland (1952), Stephenson & Wells (1955); **Heron Island,** Salter (1954).

Characters

Coralla are usually hemispherical in shape with short branches set close together. Corallites are mono- to tricentric but never form meandroid valleys (Figs. 791-793). Calices are set deep within a well-defined theca. Septa may be arranged in up to four orders in some calices but in others (often of the same colony) only two orders can be determined. In either case 30-50 per cent of the septa belong to the first order, are thicker and more exsert than the others and have regular, lobate dentations, especially towards the margin and over the theca. Dentations on the inner part of the primary septa become increasingly long and thin and the septa increasingly perforate. Septa of higher orders are thinner and have longer, finer and more irregular dentations. As

Fig. 475 Holotype of *Lobophyllia corymbosa* (× 1.0).



with other *Lobophyllia* species, the septa have finely granulated sides and finely granulated or serrated margins, especially the tops of major dentations. The columellae are usually diffuse and trabecular, but are compact in well calcified coralla. The endotheca usually plunges vertically within the calices. The walls are of constant thickness, usually approximately 4 mm. Costae are unequal and consist of low but conspicuous ridges and are frequently ornamented with spines or dentations.

Affinities

Unlike other *Lobophyllia* species, *L. corymbosa* does not have a wide range of growth form variation and is readily recognised in all environments in which it occurs. Similarities between *L. corymbosa* and other *Lobophyllia* species are discussed on pages 274 and 279.

Distribution

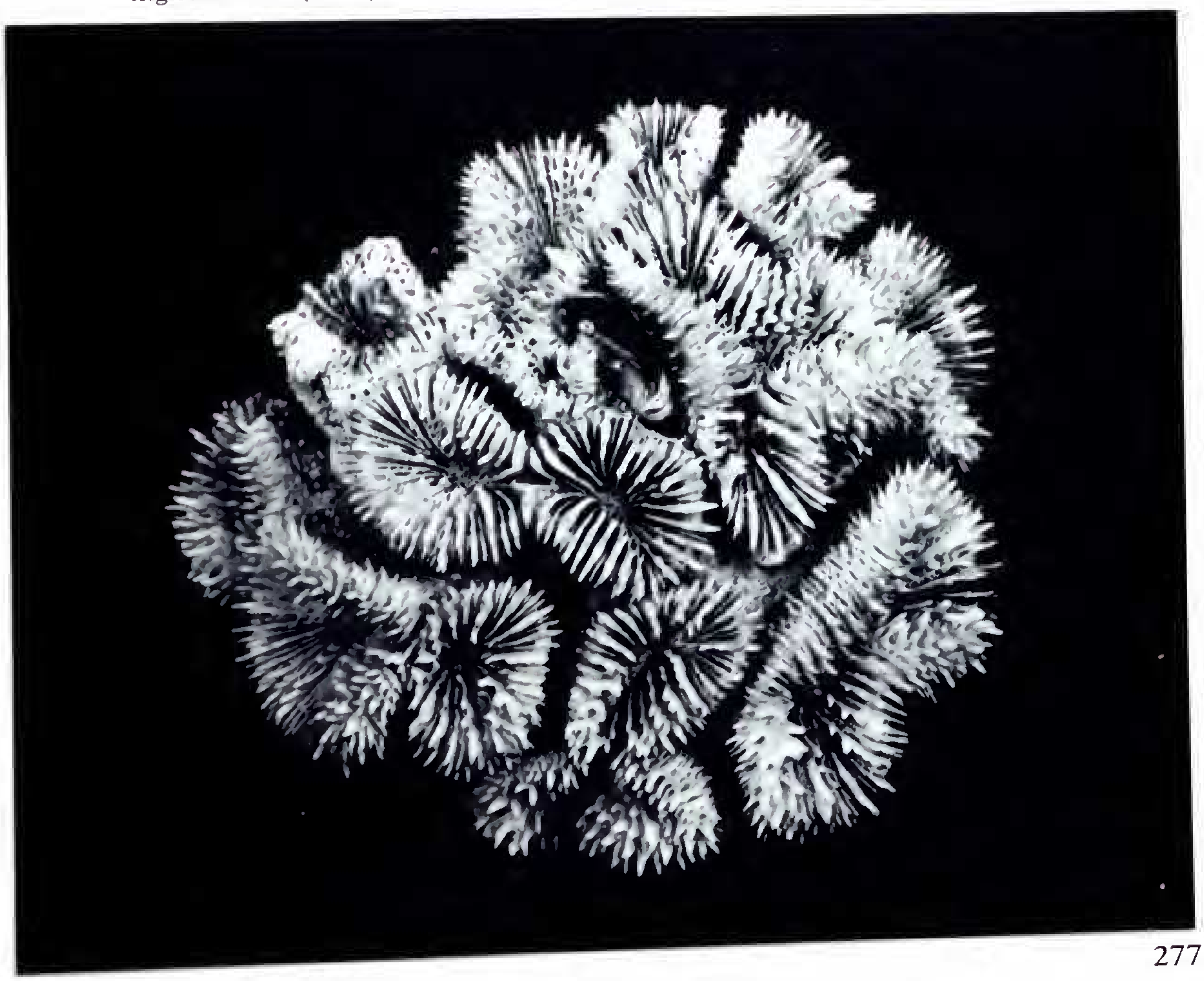
Widely distributed throughout the Indo-Pacific from the Red Sea east to Samoa, Tahiti and the Tuamotu Archipelago.

Lobophyllia pachysepta Chevalier, 1975

Synonymy

Lobophyllia pachysepta Chevalier, 1975.

Fig. 476 *Lobophyllia pachysepta* from between Orpheus and Fantome Islands, Palm Islands, collecting station 60 (× 0.8).



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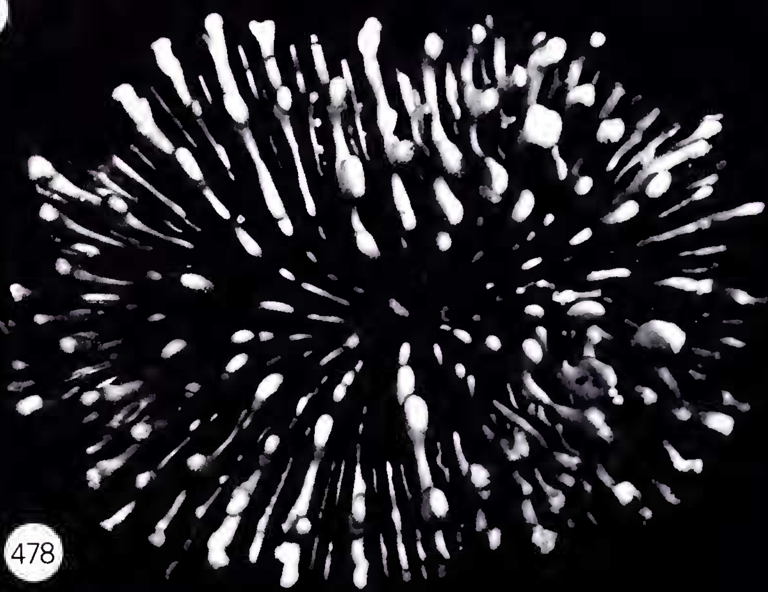

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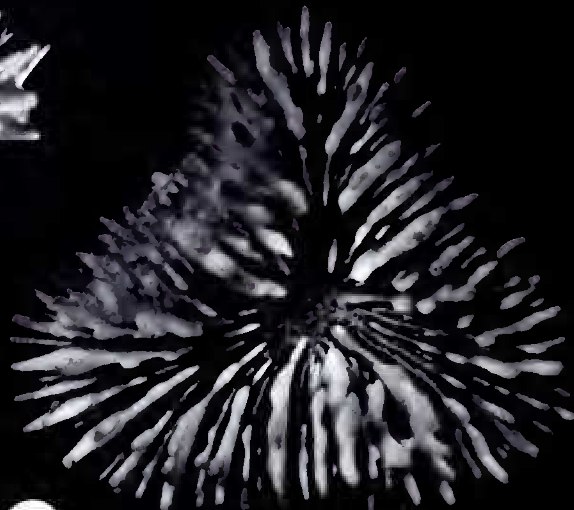

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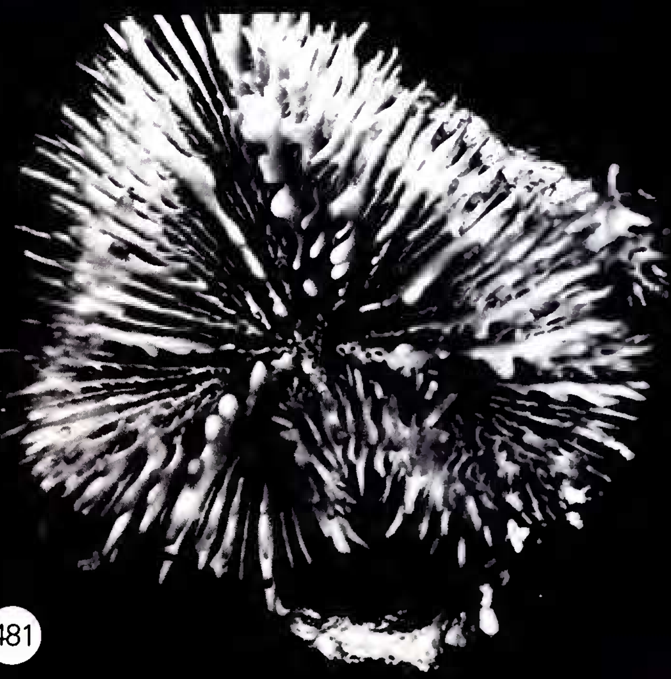


481

Material studied

Yorke Island, Lizard Island (10 specimens), **Ribbon Reef,** plug reef S of **Ribbon Reef, Hope Island, Palm Islands** (15 specimens), **Old Reef** (2 specimens), **Bait Reef** (3 specimens), **Whitsunday Islands** (3 specimens), **Bushy Island-Redbill Reef** (4 specimens), **Parker Reef** (2 specimens), **Pompey Complex** (3 specimens), **Swain Reefs** (10 specimens), **Heron Island** (2 specimens).

These localities include collecting stations 32, 33, 35, 36, 43, 45, 55, 60, 64, 65, 67, 68, 69, 70, 75, 78, 79, 80, 81, 91, 97, 98, 100, 115, 126.

Previous records from Eastern Australia

Not previously recorded.

Characters

Although this species is previously known from only a single specimen (Chevalier's holotype) it is relatively abundant throughout the Great Barrier Reef and very distinctive underwater. Coralla are phaceloid with corallites and monocentric except when in process of division. Colonies are never large; branches are short and widely spaced. Most corallites are 4-5 cm across and circular to irregular in outline. Septa are in four ill-defined orders. Those of the first order are greatly thickened with 3-5 long, irregular, lobate dentations. Septa of higher orders become increasingly thin, and have finer, more frequent dentations. All septa have fine, perforated dentations intermingled with the columellae. Those of the first order are frequently submerged in the columellae but occasionally the fine dentations extend well above the columellae. All septa have fine granulations on their sides and all dentations have granulated tops. Columellae are large and spongy and usually diffuse. Costae are poorly developed; costal spines are very echinulate. They are irregular in size and shape and are sometimes branched. The endotheca is mainly vesicular.

Living colonies are distinctive, being uniformly dark in colour with yellow or cream septal dentations (Fig. 794).

Affinities

This species comes closest to *L. corymbosa* from which it is distinguished by its greatly thickened first order septa with large lobate dentations. Underwater it is readily characterised by its colour.

Distribution

Previously recorded only from the Chesterfield Isles by Chevalier (1975), but known also from the Maldive Islands (Wells, pers. comm.).

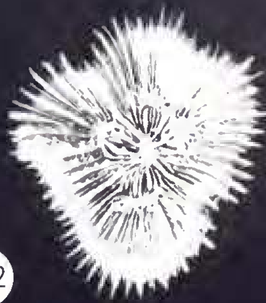
Lobophyllia hataii Yabe, Sugiyama & Eguchi, 1936

Synonymy

Lobophyllia hataii Yabe, Sugiyama & Eguchi, 1936; Ma (1937, 1959); Eguchi (1938); Nemenzo (1959); Chevalier (1975).

Figs. 477-481 *Lobophyllia pachysepta* (× 2.5).

Figs. 477, 481	From between Orpheus and Fantome Islands, Fig. 477 same corallum as Fig. 476.
Fig. 478	From Lizard Island, collecting station 33.
Fig. 479	From the Swain Reefs, collecting station 68.
Fig. 480	From the Swain Reefs, collecting station 67.



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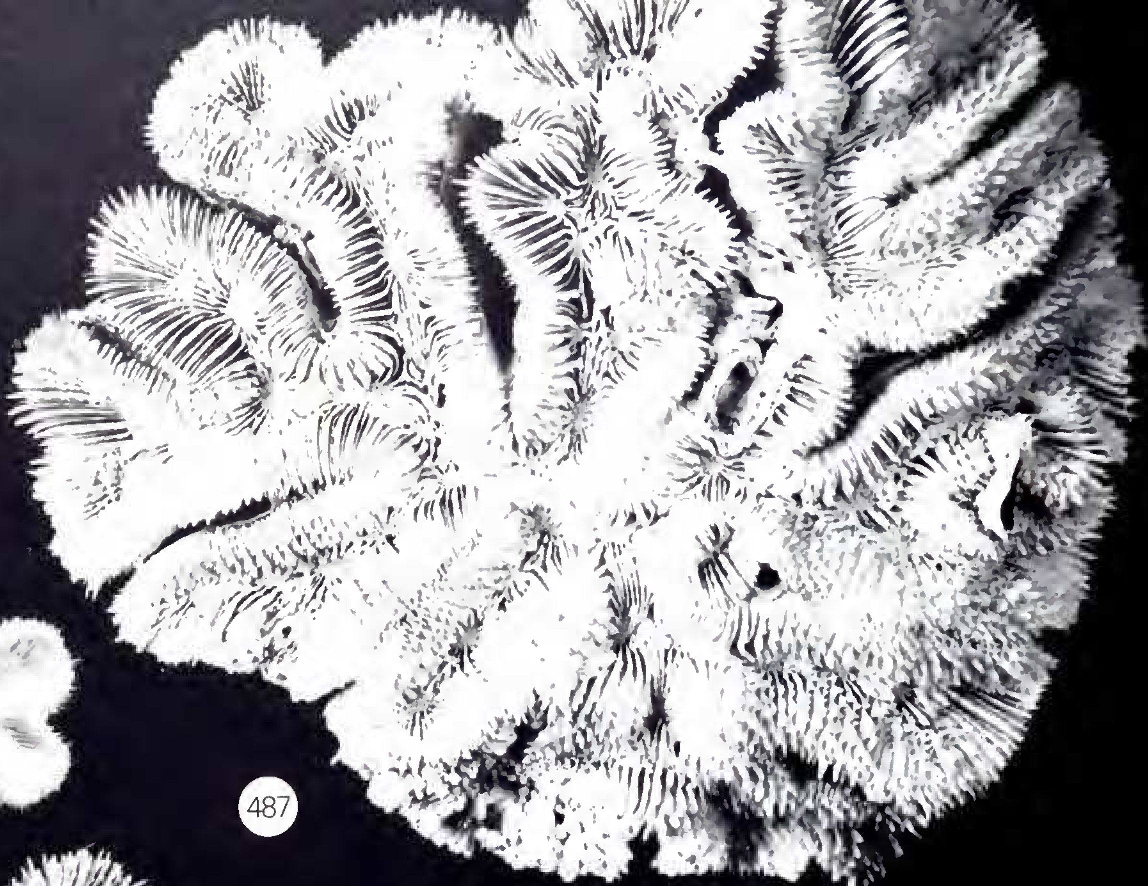

487

Material studied

Bramble Cay, Yorke Island (2 specimens), **Dungeness Reef** (13 specimens), **Murray Islands** (2 specimens), barrier reef E of **Murray Islands** (4 specimens), **Ashmore Reef** (2 specimens), **Tijou Reef, Jewell Reef, Lizard Island, Palm Islands** (4 specimens), **Bait Reef** (3 specimens), **Whitsunday Islands** (4 specimens).

These localities include collecting stations 2, 28, 32, 34, 35, 45, 80, 97, 98, 106, 108, 110, 122, 123, 125, 128, 140.

Previous records from Eastern Australia

Not previously recorded.

Characters

Coralla are partly flabellate, partly meandroid (Fig. 795). Valleys are very wide and shallow. In meandroid coralla or parts of coralla, the flat, horizontal valley floors are usually at least as wide as the collines. The latter resemble those of *Symphyllia radians* in being partly sinuous, partly radiating, and usually having a well defined, fine ambulacrum. Centres are characteristically non-axial, unlike those of other *Lobophyllia* species. The flatter and wider the valley floors, the more irregularly the centres are placed. Sometimes they occur in two distinct rows in a manner similar to *Symphyllia agaricia.* Septa are in three, usually distinct orders. Those of the first order are relatively exsert and thick and have 4-8 large echinulate or lobate dentations, the largest usually being adjacent to the columella as a paliform lobe. Third order septa are thin and scarcely exsert and have many fine, regular dentations. Second order septa are intermediate. All septa have finally granulated sides and may have finely serrated margins, especially on their dentations. Columellae are linked by 2-6 laminae which are identical in structure to the primary septa and which usually run parallel to the valley axes. There is little tendency for adjacent columellae to be linked by laminae running perpendicular to the axes. The columellae are trabecular and may be composed of only a few twisted inner septal dentations or may be large and spongy. Costae are usually present, mostly consisting of vertical rows of very elongate spines. The endotheca is very vesicular in most specimens. The edge zone is usually about 1 cm wide and valleys become separated (flabelloid) when the edge zone is extended beyond this limit. Flabelloid valleys never anastomose.

Skeletal variation and affinities

In their original description, Yabe, Sugiyama & Eguchi (1936) placed *L. hataii* in a subgenus of its own, *Palauphyllia*, distinguished by the characters of the valleys, the arrangement of the calice centres and the ornamentation of the septo-costae. In the latter respect, *L. hataii* closely resembles *L. hemprichii*, so much so that small coralla cannot be reliably distinguished. Variation in the calice structure of larger coralla also appears to be similar to that of *L. hemprichii.* Some coralla or parts of coralla of the present series have only two orders of septa, others have a tendency to form V-shaped valleys with many axial columellae.

Meandroid coralla may also show close affinities to *Symphyllia* species. As already mentioned, the non-axial distribution of columellae resembles those of *S. agaricia* but the two species are readily distinguished by the coarser septa and septal ornamentation and the much deeper valleys of *S. agaricia.*

Figs. 482-487 *Lobophyllia hattai* (× 0.5).

Figs. 482, 484 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.
Fig. 483 From Tijou Reef, collecting station 2.
Fig. 485 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.
Fig. 486 From Jewell Reef.
Fig. 487 From Wistari Reef, collecting station 117.

Lobophyllia hataii is uncommon on the Great Barrier Reef and the present series is not adequate for an analysis of growth form variation other than to note that the distinctive characters of the species appear best developed in coralla from protected biotopes.

Distribution

Previously recorded from the Maldive Archipelago, the China Sea, the Philippines, Palau and New Caledonia.

GENUS *SYMPHYLLIA* EDWARDS & HAIME, 1848

Generic synonymy

Symphyllia Edwards & Haime, 1848c; Matthai (1928); Vaughan & Wells (1943); Wells (1956); Chevalier (1975).

Type species *Meandrina sinuosa* Quoy & Gaimard, 1833 (= *Mussa nobilis* Dana, 1846).

Characters of the genus

Coralla are meandroid, with adjacent valleys united by a common wall.

Introduction

Symphyllia is a very distinct genus divided, in the Great Barrier Reef, into four species, *S.* cf. *recta*, *S. radians*, *S. agaricia* and *S.* cf. *valenciennesii.* Coralla of the first three species represent a gradient from small and sinuous to relatively coarse valleys and from fine to relatively coarse septal structures. These species, which occupy a similar range of biotopes, are of approximately equal abundance and are most common on reef faces exposed to strong wave action. The fourth species, *S.* cf. *valenciennesii*, is uncommon and has unclear affinities with other *Symphyllia* species.

Symphyllia cf. recta (Dana, 1846)

Synonymy

Meandrina sinuosa Quoy & Gaimard, 1833 (*non* Lesueur, 1821).

Mussa recta Dana, 1846.

Mussa nobilis Dana, 1846.

Symphyllia sinuosa (Quoy & Gaimard); Edwards & Haime (1849, 1857); Quelch (1886); Rehberg (1892); Gardiner (1899a, 1904); Bedot (1907); Matthai (1924).

Symphyllia recta (Dana); Matthai (1928); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Ma (1937); Eguchi (1938); Umbgrove (1939, 1940); Crossland (1952); Nemenzo (1959); Ma (1959); Scheer (1972); Scheer & Pillai (1974); Pillai & Scheer (1974).

Symphyllia nobilis (Dana); Vaughan (1918); Hoffmeister (1925); Faustino (1927); Wells (1954); Stephenson & Wells (1955); Searle (1956); Pichon (1964); Chevalier (1968, 1975).

Symphyllia hemispherica Tenison-Woods, 1879c.

Figs. 488, 489 *Symphyllia* cf. *recta* from Jewell Reef (× 0.4)


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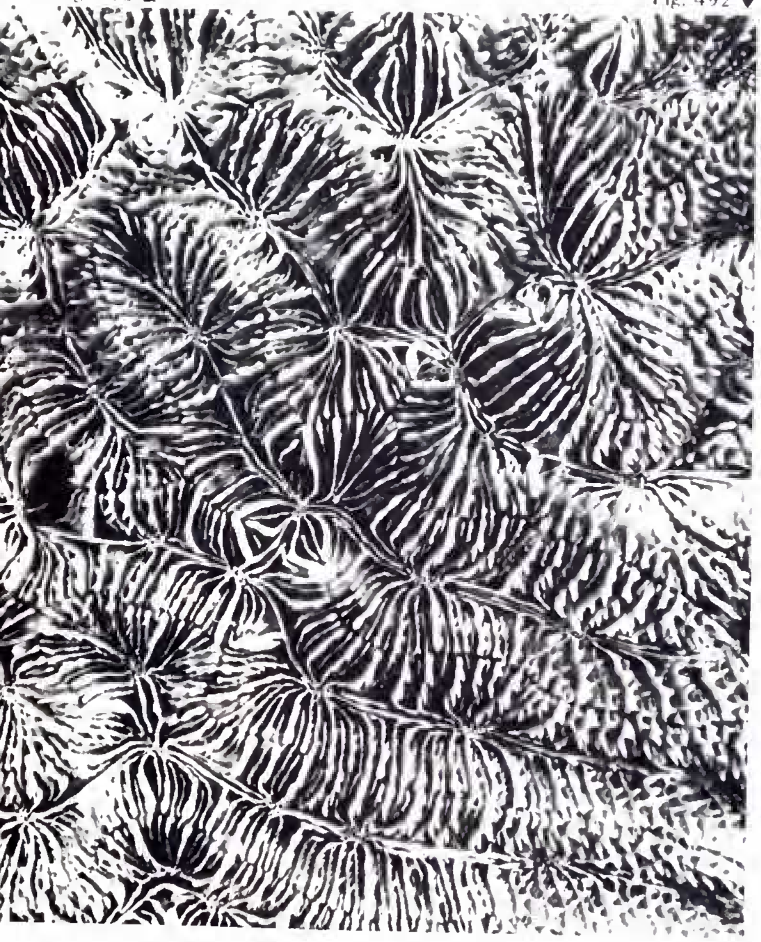
Fig. 490 ▲

Fig. 491 ▲

Fig. 492 ▼

Fig. 493 ▼



As noted by Crossland (1952), it is unfortunate that Dana's 'greatly damaged and now quite worthless specimens' were preserved and used for the revival of the names *S. recta* and *S. nobilis* as opposed to the well established *S. sinuosa.* Dana replaced the name *S. sinuosa* with *S. nobilis* because the former was based on a misidentification of Lesueur's *Meandrina sinuosa* and because (p. 188) he assigned the name *sinuosa* to a species of *Mussa.* Vaughan (1918) followed Dana, and Wells and Chevalier have subsequently followed Vaughan. However, Vaughan did not place *S. recta* in synonymy with *S. nobilis* and, as neither holotype can be identified with certainty, the present authors follow the synonymy originally proposed by Matthai where the senior of the two is given priority.

Symphyllia hemispherica from Darnley Island is almost identical to Fig. 489, an ecomorph at an extreme of the growth form variation of this species.

Material studied

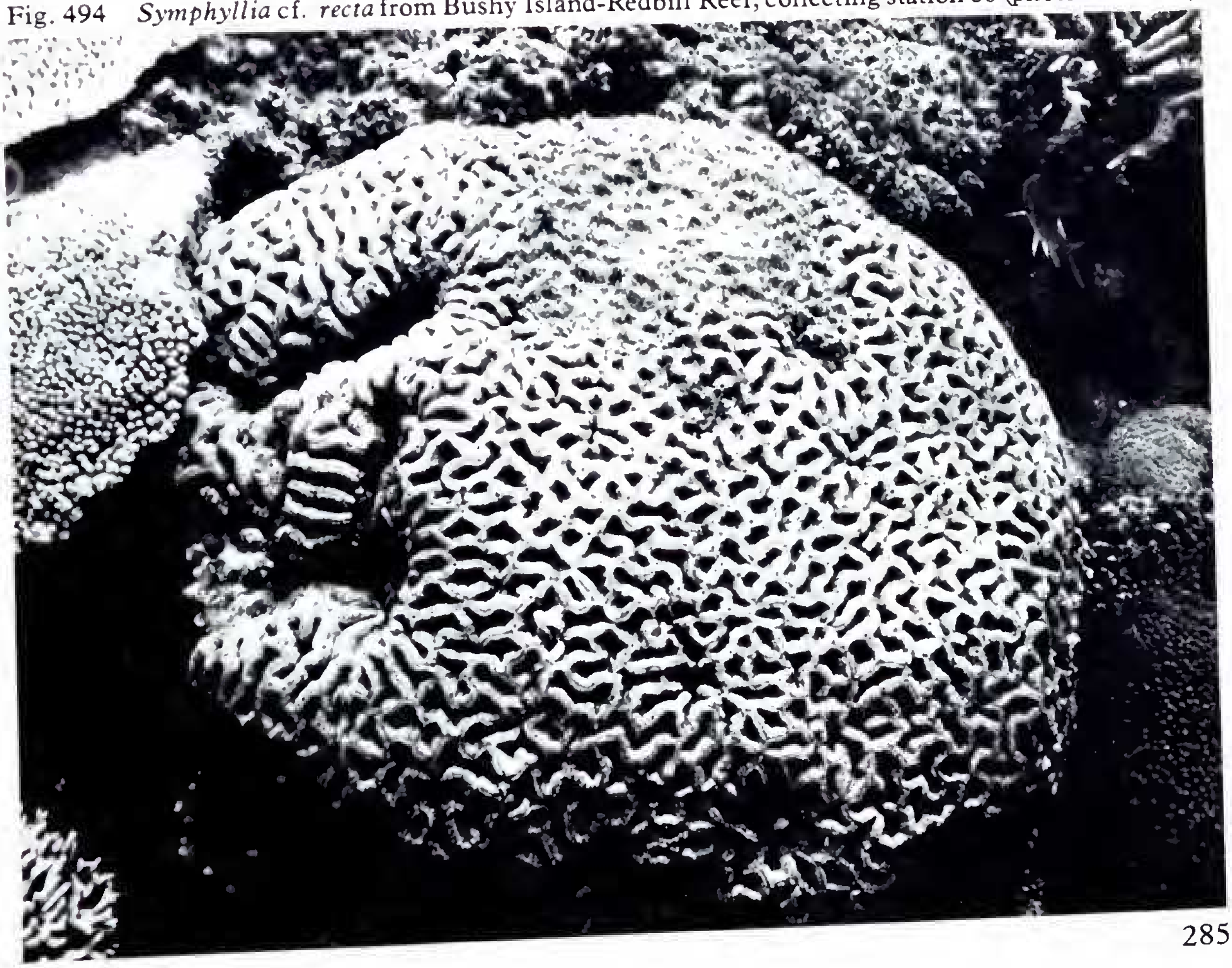
Reef 14 km NE of **Murray Islands** (2 specimens), **Triangle Reef, Great Detached Reef** (6 specimens), **Tijou Reef** (2 specimens), **Bewick Island** (5 specimens), **Houghton Island** (2 specimens), **Jewell Reef** (10 specimens), **Lizard Island** (2 specimens), **Yonge Reef, Ribbon Reef** (3 specimens), **Three Isles, Hope Island** (2 specimens), **Palm Islands** (2 specimens), **Keeper Reef, Old Reef, Swain Reefs** (2 specimens), **Heron Island.**

These localities include collecting stations 1, 2, 5, 7, 9, 18, 32, 33, 40, 41, 43, 61, 63, 65, 69, 79.

Figs. 490-493 *Symphyllia* cf. *recta* (× 1.0).

Fig. 490 From Jewell Reef, same corallum as Fig. 488.
Fig. 491 From Triangle Reef.
Figs. 492, 493 From Jewell Reef, both the same corallum as Fig. 489.

Fig. 494 *Symphyllia* cf. *recta* from Bushy Island-Redbill Reef, collecting station 80 (photo: T. Done).



Previous records from Eastern Australia

Murray Islands and vicinity (as *S. nobilis*) Vaughan (1918), Mayer (1918); **Torres Strait,** Matthai (1928); **Thursday Island,** Matthai (1928); **Low Isles,** Yonge (1930), Marshall & Orr (1931), Yonge & Nicholls (1931), Yonge *et al.* (1932), Marshall & Stephenson (1933), Stephenson & Stephenson (1933) (as *Symphyllia*) Stephenson *et al.* (1931), Manton (1935), (as *S. nobilis*) Crossland (1952), Stephenson & Wells (1955); **Heron Island** (as *S. nobilis*) Salter (1954).

Characters

As with other *Symphyllia*, colonies form low domes or are nearly hemispherical. Valleys are very sinuous and ramify in an irregular fashion. Septa are arranged in two alternating orders or three indistinct, irregular orders. First order septa are thick, especially on their upper margins where they are strongly dentate. The dentations decrease in size towards the valley centres and the septa taper, sometimes abruptly. Higher order septa are thin and less coarsely dentate. Many do not reach the columellae; they either end abruptly or anastomose. The columellae are usually small and are mostly made up of the inner ends of primary septa twisted together in a clockwise direction. Columella centres are usually spaced at regular intervals of approximately 16 mm in the centre of the valleys. They are linked by 3 or 4 laminar linkages which run lengthwise along the valley and which have the same structure and appearance as the septa, with dentations more prominent at their centres rather than their extremities. Septa of adjacent valleys are not adjoined and most specimens of the present series have a well defined ambulacral groove along the top of the colline. The latter is usually thick and rounded. The costae usually do not extend far down the edge zone, which is usually ornamented with sharp spines. The endotheca is vesicular and well developed.

Living colonies vary greatly in colour but are mostly dull brown, greys and greens, sometimes red (Fig. 796).

Skeletal variations

Symphyllia cf. *recta ecomorph hemispherica.*

Coralla from very exposed biotopes, of which Fig. 489 is an extreme case, show substantial deviation from those described above. Valleys tend to be short, even monocentric, with individual corallites very irregular in shape. Primary septa have greatly thickened upper margins and taper abruptly. They are strongly dentate with 1-3 dentations being very prominent. Septa of higher orders are highly anastomosed. Columellae are usually well developed but diffuse, even extending the full length of valley floors. They are trabecular and usually echinulate. Valleys are relatively deep with acute collines.

Symphyllia cf. *recta from semi-protected biotopes.*

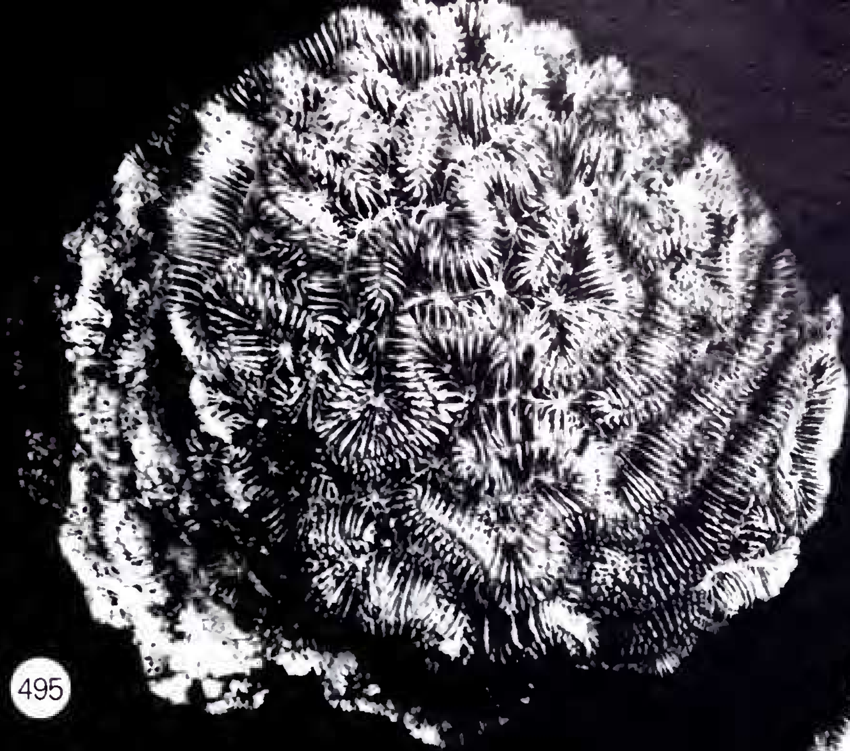
This species has not been found in turbid water. Coralla obtained from what appear to be minimal environmental conditions differ from the general description in having very shallow valleys with thin, almost uniform septa and scarcely developed columellae. The endotheca is very vesicular.

Affinities

Symphyllia cf. *recta* is closest to *S. radians*. It is distinguished by its smaller, more sinuous valleys, finer septal dentations and by differences in septal ornamentation.

Figs. 495-498 *Symphyllia radians* (× 0.5).

Fig. 495 From Jewell Reef.
Fig. 496 From Frigate Cay, Swain Reefs, collecting station 81.
Fig. 497 From Jewell Reef, collecting station 61.
Fig. 498 From Lizard Island, collecting station 32.



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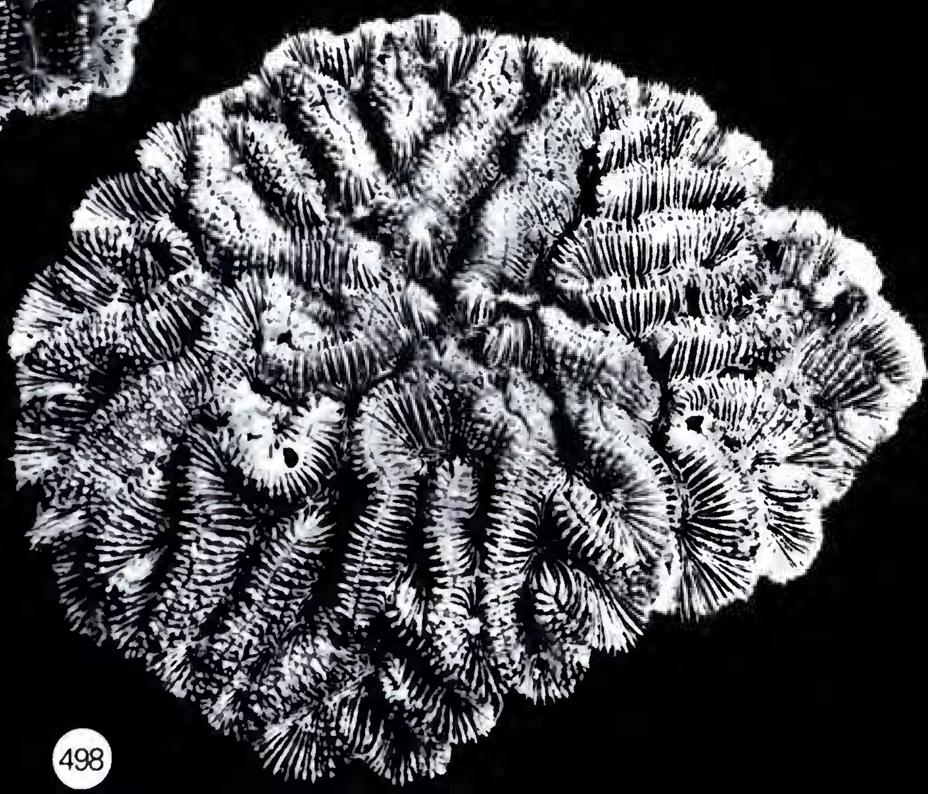

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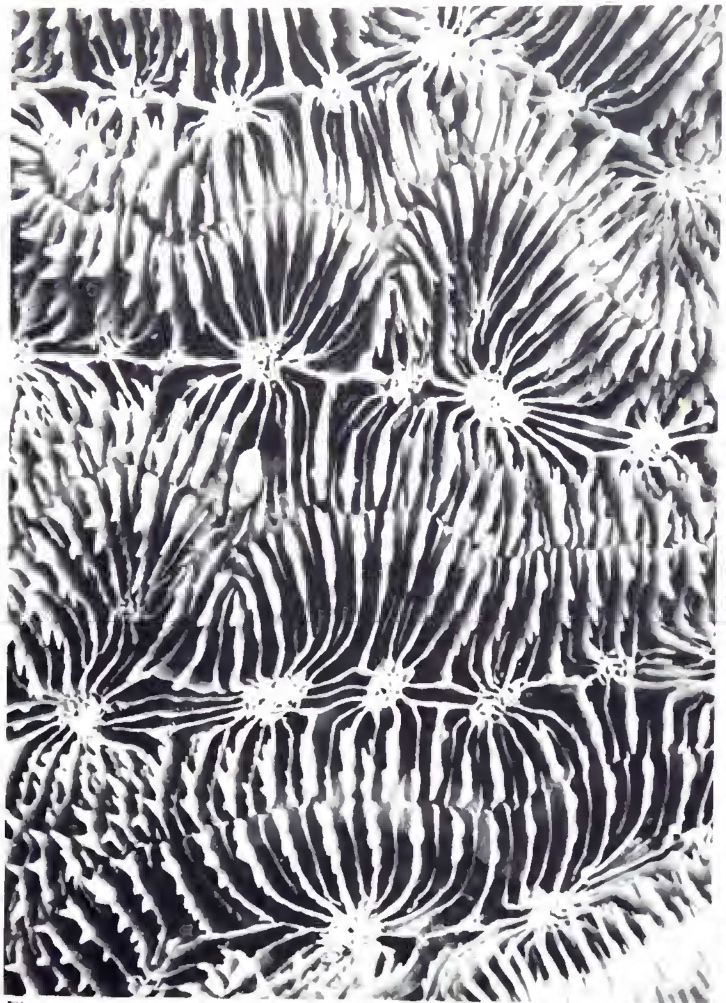

Fig. 499 ▲

Fig. 501 ▼

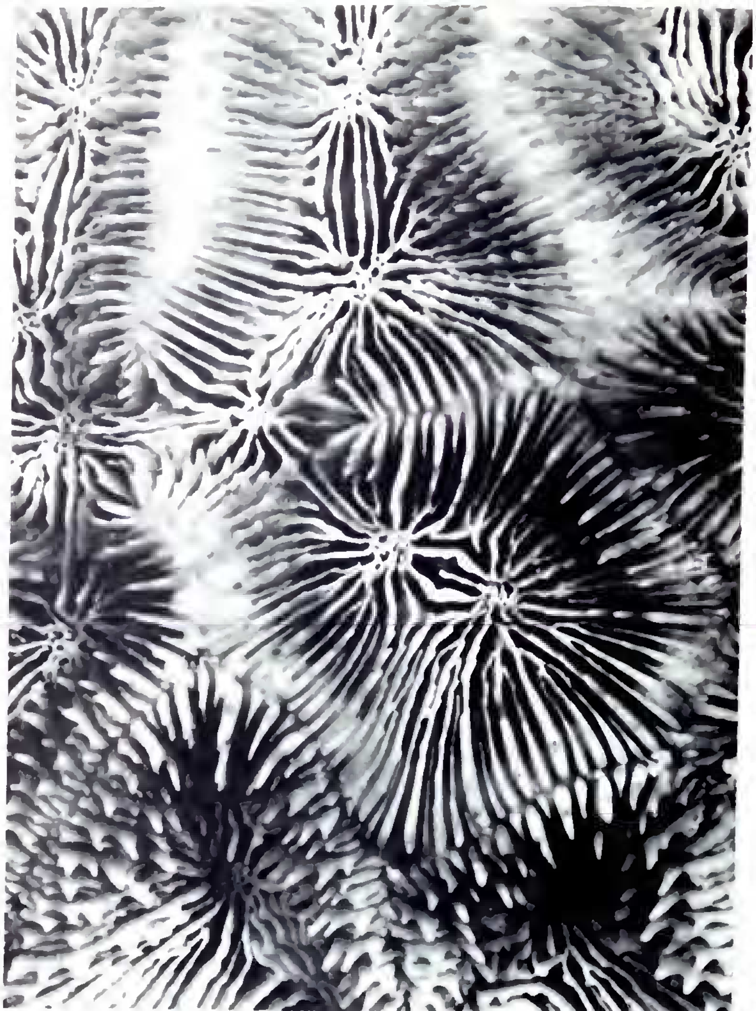

Fig. 500 ▲

Fig. 502 ▼

Distribution

Recorded from the Maldive Islands, throughout the tropical eastern Indian Ocean to the Western Pacific as far east as the Marshall Islands and Samoa.

Symphyllia radians Edwards & Haime, 1849

Synonymy

Mussa crispa Dana, 1846; *non Meandrina crispa* Lamarck (1816).

Symphyllia radians Edwards & Haime, 1849a; Edwards & Haime (1857); Verrill (1864); Studer (1881); Ortmann (1888); Matthai (1924, 1928); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1940); Crossland (1952); Nemenzo (1959); Scheer & Pillai (1974); Chevalier (1975).

Symphyllia grandis Edwards & Haime, 1849a; Edwards & Haime (1857); Studer (1881).

The holotype of *S. grandis* has thin, exsert, very irregular primary septa. It is lightly calcified and has a vesicular endotheca and thus shows resemblance to Great Barrier Reef *S. radians* from partly protected biotopes.

Matthai (1928) placed *S. indica* Edwards & Haime in synonymy with *S. radians.* However, a specimen labelled 'holotype' in the Paris Museum shows closer resemblance to *S. agaricia.*

Material studied

Dungeness Island, barrier reef E of **Murray Islands, Great Detached Reef** (13 specimens), **Tijou Reef** (3 specimens), **Bewick Island, Houghton Island, Jewell Reef** (12 specimens), **Lizard Island** (4 specimens), **Ribbon Reef** (3 specimens), **Hope Island** (3 specimens), **Three Islands, Low Isles** (3 specimens), **Palm Islands** (10 specimens), **Magnetic Island, Old Reef** (2 specimens), **Whitsunday Islands** (2 specimens), **Swain Reefs** (6 specimens).

These localities include collecting stations 1, 2, 5, 6, 18, 32, 36, 37, 40, 41, 57, 61, 63, 65, 68, 69, 79, 81, 94, 98, 110, 122.

Previous records from Eastern Australia

Low Isles, Crossland (1952), Stephenson & Wells (1955); **Solitary Islands,** Veron *et al.* (1974).

Characters

Colonies are hemispherical to flat. Valleys are mostly irregularly sinuose in hemispherical or dome-shaped coralla and relatively straight and radiating in flat coralla. They are of indefinite length. Branches form when the valley width exceeds approximately 22 mm (up to 27 mm in coralla from protected biotopes). As with other *Symphyllia* species, septa are not clearly arranged in orders although up to 4 orders can sometimes be distinguished. More commonly there are either thick or thin septa which alternate or otherwise occur in constant proportion, especially in straight valleys. Thick (first order) septa are strongly dentate, 3-6 major dentations usually occurring along the septal margin, most conspicuously the upper half. Higher order septa are thinner and have finer, more numerous dentations. The development of the columellae varies greatly among different coralla, from a few twisted, flat or echinulate trabeculae, to a fully spongiose condition. Columellae usually form in the

Figs. 499-502 *Symphyllia radians* (× 1.0).

Figs. 499-501	From Jewell Reef, same coralla as Figs. 495-497 respectively.
Fig. 500	From Frigate Cay, same corallum as Fig. 496.
Fig. 502	From Lizard Island, same corallum as Fig. 498.

centre of the valleys, except those in the process of branching, and are linked by laminar linkages running lengthwise along the valley. The latter usually have well developed dentations and are frequently joined by septa. There is almost always a well defined ambulacral groove running along the top of the collines. The endotheca is usually vesicular. The edge zone is irregularly covered with spines as in other *Symphyllia* species and costae are poorly developed.

Living colonies (Fig. 797) may be very colourful, frequently with valleys and walls being different. There are no common or characteristic colour combinations.

Skeletal variation

Most of the range of variations of the present series is illustrated in Figs. 499-502. The main source of variation is in the relative width of the walls and valleys. Coralla from more protected biotopes tend to have narrow walls with relatively thin primary septa as do other *Symphyllia* species.

Affinities

This species can be readily distinguished from other *Symphyllia* underwater and in collections from similar biotopes, but in large collections some coralla may come close to *S. agaracia* (see p. 293) and, more particularly, *S.* cf. *recta*. The latter does not have valleys arranged in a radiating pattern; valleys are usually more sinuous and are always smaller. *S. radians* has larger septal dentations although not as large as *S. agaricia*. The latter species can usually be reliably distinguished by the two rows of columella centres and larger valleys (see Figs. 508, 510).

Distribution

The present recorded distribution is from the Laccadive and Maldive Islands east to New Caledonia and Rotuma.

Symphyllia agaricia Edwards & Haime, 1849

Synonymy

Symphyllia agaricia Edwards & Haime, 1849a; Ortmann (1888); Matthai (1924, 1928); Yabe & Sugiyama (1935); Yabe, Sugiyama & Eguchi (1936); Nemenzo (1959); Scheer & Pillai (1974).

Symphyllia acuta Quelch, 1886; Bedot (1907).

Symphyllia indica Edwards & Haime, 1849a.

Material studied

Murray Islands, Great Detached Reef, Tijou Reef (2 specimens), **Jewell Reef** (2 specimens), **Lizard Island** (4 specimens), **Ribbon Reef** (4 specimens), **Palm Islands** (2 specimens), **Bait Reef, Whitsunday Islands, Parker Reef** (2 specimens), **Swain Reefs** (3 specimens).

These localities include collecting stations 1, 2, 29, 32, 33, 34, 60, 65, 69, 81, 98, 100.

Previous records from Eastern Australia

Palm Islands, Matthai (1928); **Heron Island**, Salter (1954).

Figs. 503-506 *Symphyllia agaricia* (× 0.4).

Figs. 503, 506 From Jewell Reef.
Fig. 504 From Ribbon Reef, collecting station 65.
Fig. 505 From between Orpheus and Fantome Island, Palm Islands, collecting station 60.

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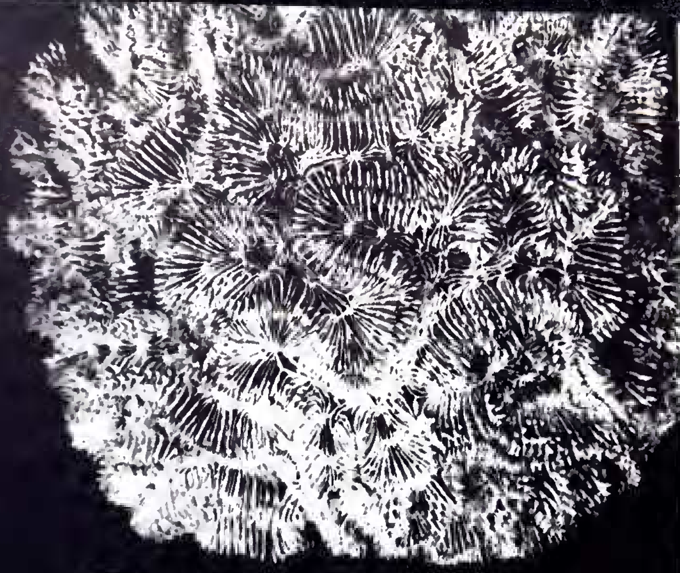

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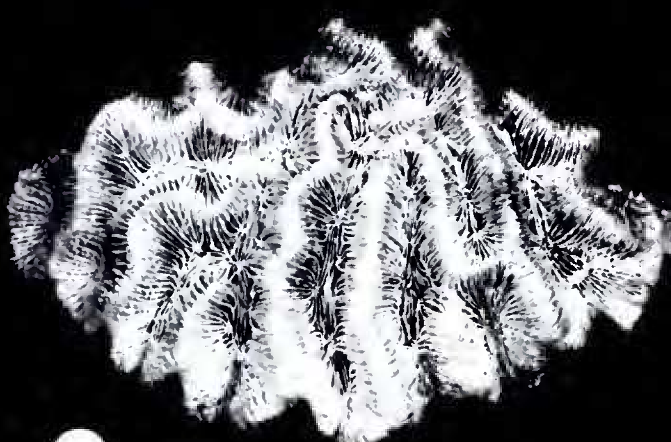

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Fig. 507 ▲

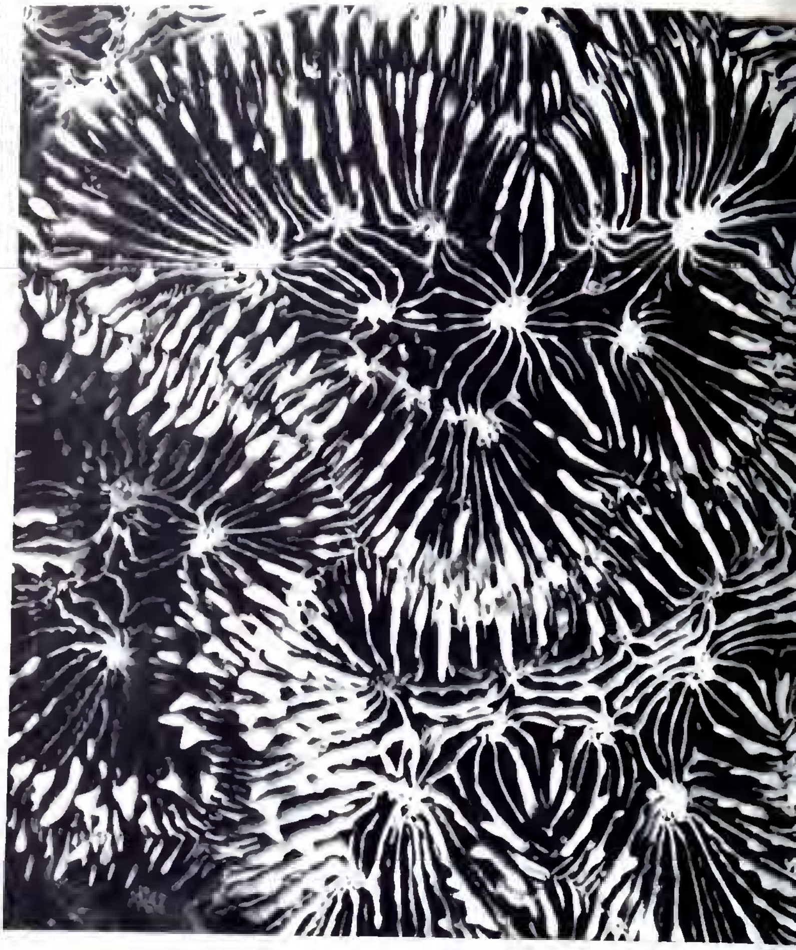
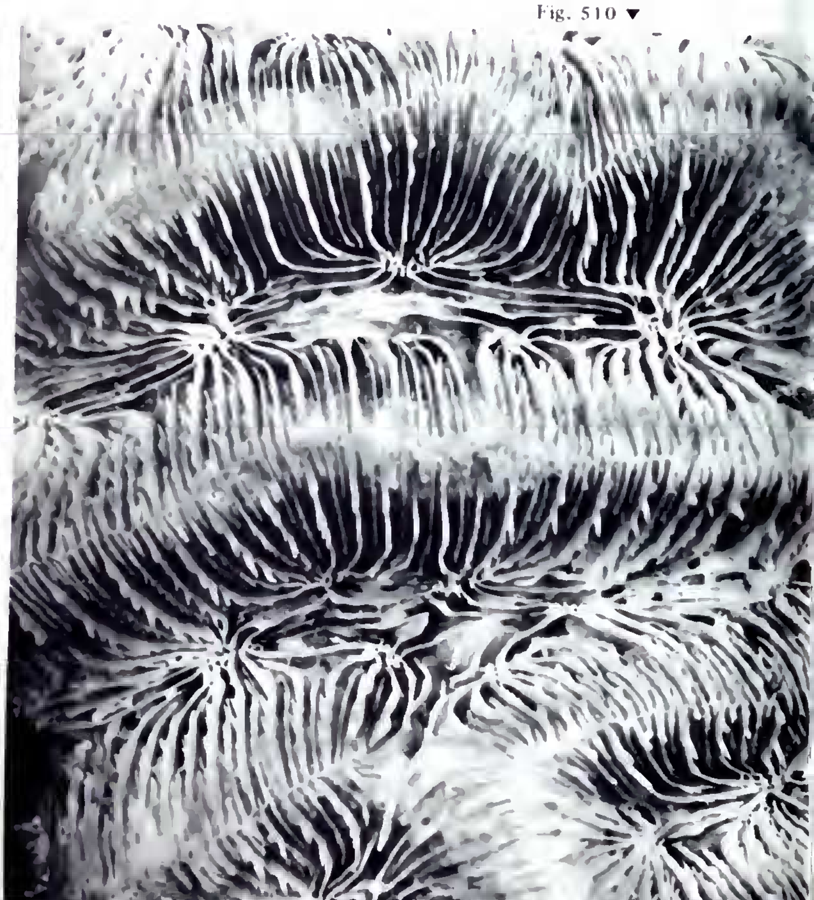


Fig. 508 ▲

Fig. 509 ▼

Fig. 510 ▼



Characters

Valleys are of indefinite length, sinuous or radiating and are very wide (averaging 35 mm) with 8-10 septa per cm. These vary greatly in thickness from approximately 1 mm to very fine lamellae, but are not arranged in distinct orders. Principal septa are thick and have very coarse dentations. The number of dentations increases as the width of the septa decreases. Columellae are arranged in two rows, longitudinally connected by 2-6 evenly spaced, well developed, lamellar linkages. One or two lamellar linkages may adjoin adjacent centres within valleys; otherwise they are completely separated by lamellar linkages running along the valley centre. Columellae are seldom well developed and consist largely of the inner margins of septa twisted together, usually in a clockwise direction. The endotheca is vesicular and well developed.

The walls of adjacent valleys are usually well separated at the growing edges of colonies, and have costae extending down the edge zone. When adjacent valleys become fused, corresponding septa are seldom regularly adjoined. A fine lamellar ridge running down the top of the collines usually links all septa.

Living colonies (Fig. 798) are uniform brown, green or red or are composed of two colours. They are readily recognised underwater.

Skeletal variation

This species may be abundant on the outer slopes of barrier reefs where coralla, if exposed to strong wave action, have extremely dentate primary septa separated by 2-4 second order septa which are much thinner and more finely dentate. One such specimen in the present series has well developed centres extending down the centre of the valley floor with small, secondary centres arranged on either side.

Coralla from more protected biotopes have more evenly developed septa and columellae. Septa are more widely spaced and lamellar linkages more diffuse.

Affinities

Symphyllia agaricia is well characterised by the double row of columella centres, the width of the valleys and coarseness of the septal dentations. Parts of some *S. radians* and *S.* cf. *valenciennesii* colonies may show some tendency to form double columella rows but this never occurs to the extent normally found in *S. agaricia*. Matthai (1928) appears to be correct in synonymising *S. acuta* with *S. agaricia* as the former also has a double row of centres.

Distribution

Widely distributed from the western Indian Ocean to Samoa.

Symphyllia cf. valenciennesii Edwards & Haime, 1849

Synonymy

Symphyllia valenciennesii Edwards & Haime, 1849a; Edwards & Haime (1857); Matthai (1924, 1928); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1940); Ma (1959); Chevalier (1975).

Symphyllia hassi Pillai & Scheer, 1976.

Symphyllia hassi, decribed from a single specimen, is very similar to several specimens of the present series and to Chevalier's figure (Pl. XXVI, Fig. 4) of *S.*

Figs. 507-510 *Symphyllia agaricia* (× 1.0).

Figs. 507, 510 From Jewell Reef, same coralla as Figs. 503, 506 respectively.
Fig. 508 From Ribbon Reef, same corallum as Fig. 504.
Fig. 509 From between Orpheus and Fantome Islands, Palm Islands, same corallum as Fig. 505.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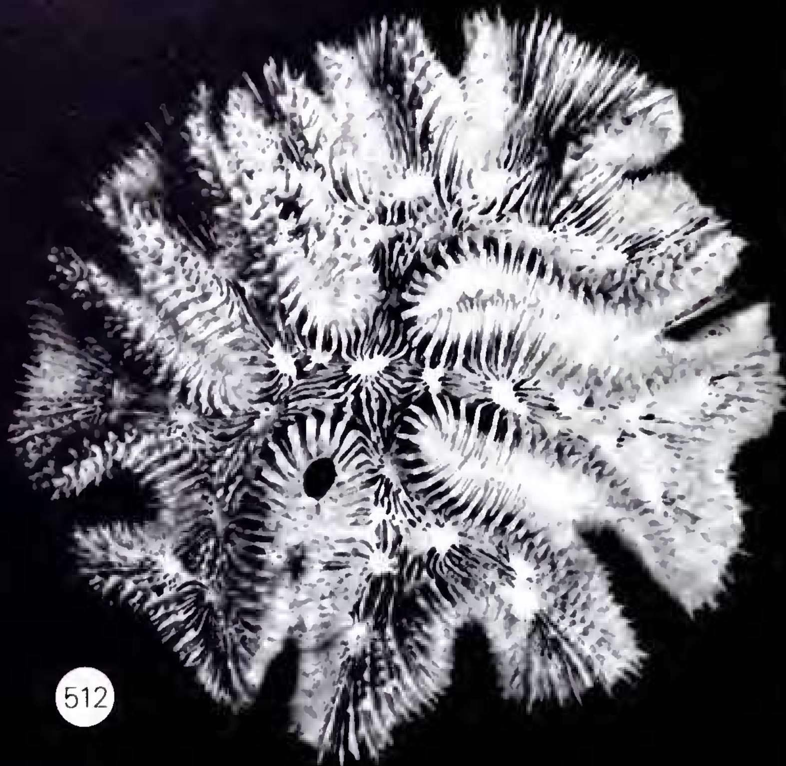
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valenciennesii. Pillai & Scheer noted (p. 66) that '*S. valenciennesii* and *S. agaricia* are characterised by two rows of columella centres in the valleys; the former differing from the latter by the presence of a deep groove on the colline. But none of the earlier species has a solid columella surrounded by paliform lobes'. The present series, however, shows some development of paliform lobes and some tendency to form a double row of columellae and it should be noted that a double row of columellae is not clearly developed in Edwards & Haime's series (Matthai, 1928, Pl. 32, Fig. 1). Nevertheless, there remains some doubt that this species is the same as that of Edwards & Haime, a question that can only be resolved by further study of specimens from the type locality (Singapore).

Material studied

Campbell Island, Big Mary Reef (4 specimens), **Yorke Island** (3 specimens), **Dungeness Reef** (2 specimens), **Murray Islands**, barrier reef E of **Murray Islands** (2 specimens), **Aureed Island, Whitsunday Islands** (2 specimens), **Wistari Reef.**

These localities include collecting stations 28, 110, 117, 122, 123, 125, 131, 132, 133.

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies are usually flat or dome-shaped. Valleys radiate from a central area which may be up to 7 cm in diameter (Figs. 511, 799). They are mostly straight, very wide (averaging 4 cm) and have steep sides and horizontal floors. There are 6-8 septa per cm. Like *S. agaricia*, these vary greatly in thickness but are not arranged in consistent orders. Principal septa are very coarse, up to 2 mm thick and commonly 12 mm exsert. Other septa become increasingly thinner, more finely dentate and much less exsert. Columellae are conspicuous; they are up to 10 mm across and are compact and spongy. They are linked with up to 7 dentate laminae, identical in structure to the minor septa and occasionally to the principal septa. The innermost septal dentation is the largest and paliform crowns are developed in some coralla. In flat central areas of some coralla, calices may be radially symmetrical with up to 23 laminar linkages taking the form of septo-costae. There are usually deep grooves between adjacent valleys. As previously noted, there is some tendency to form a double row of columellae, usually in the wider parts of valleys. This tendency is not as pronounced as in *S. agaricia*. Irregular costae extend down the sides of these grooves, but are seldom adjoined.

Skeletal variation

Some coralla of the present series are very similar to Pillai & Scheer's figure of the holotype of *S. hassi* while others show more of the characters of the *S. valenciennesii* of Edwards & Haime. These characters are largely dependent on the stage of growth of the colony; small colonies show little development of valleys and large colonies show increasing *Lobophyllia*-like separation of valleys. As with most mussid species, coralla from clear, shallow water are more calcified than those exposed to less light and have thicker, more exsert septa. It is emphasised, however, that this species is uncommon, and that the present series is unlikely to indicate its full range of variation.

Figs. 511-514 *Symphyllia* cf. *valenciennesii*, Figs. 511-513 (× 0.5).

Fig. 511 From Parker Reef.
Fig. 512 From Dungeness Reef, collecting station 122.
Figs. 513, 514 From Big Mary Reef, collecting station 131.

Affinities

Symphyllia cf. *valenciennesii* is closest to *S. agaricia,* although it is easily distinguished by the absence of two clearly developed rows of columellae, the presence of the groove down the collines, and the presence of flat, wide valley floors, especially around the corallum centre. There are also similarities with some *Lobophyllia* species. Immature colonies may show resemblances to *L. hataii.* Both have flat valley floors and may have open central areas with little valley formation. In such cases, *L. hataii* is distinguished by its finer septo-costae and usually there is a more pronounced development with two rows of columellae. There is little similarity between mature colonies of these species.

Distribution

Specimens attributed to this species range from Aldabra in the western Indian Ocean east to New Caledonia and Tonga.

IX
Family Pectiniidae Vaughan & Wells, 1943

The Pectiniidae of Vaughan & Wells (1943) are composed of five extant, colonial, hermatypic genera, *Echinophyllia, Oxypora, Mycedium, Pectinia* and *Physophyllia* and one fossil, solitary genus, *Fungophyllia* Gerth, 1923. The recent genera were previously divided into three separate families, Echinoporidae (including *Mycedium, Oxyphillia = Echinophyllia*, as well as the faviid genus *Echinopora*), Tridacophyllidae (including *Tridacophyllia = Pectinia*, and *Physophyllia*) and Oxyporiidae (*Oxypora*) by Yabe *et al.* (1936).

The Pectiniidae mostly have very thin skeletal structures with corallites usually lacking definite walls and septa which are irregularly dentate and formed from one fan system of compound trabeculae. Columellae are usually weakly developed. Costae are always well developed and the coenosteum characteristically lacks ornamentation.

GENUS *ECHINOPHYLLIA* KLUNZINGER, 1879

Generic synonymy

Echinophyllia Klunzinger, 1879; Wells (1936b, 1956); Vaughan & Wells (1943).

Oxyphyllia Yabe & Eguchi, 1935a.

Type species *Madrepora aspera* Ellis & Solander, 1786.

Introduction

Despite the small number of species involved, the relationships between *Echinophyllia* and other genera of the Pectiniidae have long remained a subject of doubt and disagreement. Yabe & Eguchi (1935a) distinguished two 'distinct forms', one 'quite identical to *Physophyllia ayleni* Wells . . . the other . . . coincided with in all respects *Madrepora aspera* Ellis & Solander' (p. 376). For the latter they erected a new genus, *Oxyphyllia*, on the basis that *Trachypora* Verrill and *Echinophyllia* Klunzinger were both junior synonyms of *Oxypora*. Despite this mistake (see p. 314) and despite confusion with *Echinopora* (Family Faviidae), the relationships of *E.* (= *Oxyphyllia*) *aspera* to other Pectiniidae were initially recognised. 'In the general features of the corallum and particularly of its surface, *Oxyphyllia* resembles superficially *Oxypora*, but is easily distinguished from it by barely costated base and the absence of slit-like pores characterising *Oxypora*. In the former feature *Oxyphyllia* is allied with *Mycedium, Echinopora* and *Physophyllia*, but differs from them in the following respects: *Mycedium* having more or less naked septocostae and inclined calices, *Echinopora* smaller spines and smaller calices surrounded by well developed circular walls, and *Physophyllia* larger calices, larger interseptal loculi, subentire septal and septocostal borders and characteristic dissepimental wall.'

In great contrast Matthai (1948a) concluded that '*Echinophyllia* is probably descended from a *Podabacia*-like ancestor'. He pointed out characters which he believed united *Podabacia, Doderleinia, Halomitra* and *Echinophyllia* and summarised his findings with an evolutionary tree uniting these genera with *Pachyseris* and *Pavona* and more distantly with other genera of the Fungiidae.

Vaughan & Wells (1943) created the Family Pectiniidae, including in it the genera recognised by most subsequent authors including the present ones. However, it was

not till the time of Wells (1954) and Nemenzo (1959) that these genera were discussed at a specific level, both authors placing only one species, *E. aspera*, in *Echinophyllia*. Wells concluded that 'the only real difference between *Echinophyllia* and *Mycedium* is in the attitude of the calicular centres: parallel in the former and inclined peripherally in the latter . . . the resemblance between the present facies (*E. aspera* series) and *M. tenuicostatum* is obvious. Further study is needed to clarify the status of these closely allied if not identical genera'.

Chevalier (1975) included four species in *Echinophyllia: E. aspera, E. rugosa* n. sp., *Oxypora glabra* Nemenzo and *Pectinia echinata* Saville-Kent, and partly redefined the characters of the genus to accommodate them. These forms are all clearly represented in the present collection although only two, *E. aspera* and *E. echinata*, are included in *Echinophyllia. Oxypora glabra* is replaced in the genus *Oxypora* and *E. rugosa* is believed to be a possible synonym of *O. lacera*.

Echinophyllia aspera (Ellis & Solander, 1786)

Synonymy

Madrepora aspera Ellis & Solander, 1786.

Echinopora aspera (Ellis & Solander); Dana (1846); Edwards & Haime (1857).

Fig. 515 *Echinophyllia aspera* from Lord Howe Island, collecting station 145 (× 0.4)

Figs. 516-519 *Echinophyllia aspera* (× 5.0).

Fig. 516 From Wistari Reef.
Fig. 517 From between Haslewood and Whitsunday Islands, collecting station 94.
Fig. 518 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.
Fig. 519 From Bullumbooroo Bay, Great Palm Island, collecting station 35.

Fig. 516 ▲

Fig. 517 ▲

Fig. 518 ▼

Fig. 519 ▼

Echinophyllia aspera (Ellis & Solander); Klunzinger (1879); Matthai (1948a, 1948b); Wells (1954); Nemenzo (1959); (*pars*) Chevalier (1975); (*pars*) Pillai & Scheer (1976).

Oxyphyllia aspera (Ellis & Solander); (*pars*) Yabe & Eguchi (1935a); (*pars*) Yabe, Sugiyama & Eguchi (1936).

non Mycedium aspera (Ellis & Solander); Matthai (1924).

non Oxyphyllia aspera var. *tosaensis* Yabe & Eguchi, 1935a; Yabe, Sugiyama & Eguchi (1936).

non Oxyphyllia aspera var. *sugiyamai* Yabe & Eguchi, 1935a; Yabe, Sugiyama & Eguchi (1936); (*pars*) Ma (1959).

non Oxyphyllia aspera (Ellis & Solander); Umbgrove (1939).

non Oxypora aspera (Ellis & Solander); Crossland (1952).

non Echinophyllia aspera var. *tosaensis* (Yabe & Sugiyama); Chevalier (1975).

non Echinophyllia aspera var. *sugiyamai* (Yabe & Sugiyama); (*pars*) Ma (1959); Pillai & Scheer (1976).

Wells (1954) placed two other species in his synonymy of *E. aspera: Tridacophyllia echinata* Saville-Kent (1871) and *Echinopora magna* Gardiner (1904). These are considered a separate species by Chevalier (1975) and the present authors.

As indicated above, many specimens have been incorrectly referred to *E. aspera* by previous authors, usually under the varieties *tosaensis* and *sugiyamai*, following Yabe *et al.* (1936). Most of these belong to *E. orpheensis* described below (p. 302). Fortunately, the clear illustration of Ellis & Solander (1786) allows no doubt about the identity of *E. aspera.* It is also clearly illustrated by Yabe *et al.* (1936) (Pl. 36, Figs. 1, 2); Wells (1954) (Pl. 176, Figs. 1-5); Chevalier (1975) (Pl. 34, Fig. 2) and Pillai & Scheer (1976) (Pl. 30, Fig. 1).

Material studied

Jervis Reef (2 specimens), **Murray Islands** (3 specimens), **Dungeness Reef, Sue Island, Thursday Island** (3 specimens), **Wai Weer Island, Tijou Reef, Lizard Island** (2 specimens), **Palm Islands** (10 specimens), **Parker Reef, Whitsunday Islands** (6 specimens), **Pompey Complex, Swain Reefs** (4 specimens), **Wistari Reef, Heron Island, Lord Howe Island** (2 specimens).

These localities include collecting stations 6, 17, 33, 34, 35, 36, 37, 39, 42, 45, 54, 60, 69, 75, 79, 83, 94, 97, 98, 109, 115, 119, 122, 135, 137.

Previous records from Eastern Australia

Heron Island, Stephenson & Wells (1955); **Lord Howe Island,** Veron (1974).

Characters

Large colonies (e.g. Fig. 520) are frequently composed of a complex of irregular, frequently overlapping plates surrounding irregular, hillocky or submassive central areas. Smaller coralla (Fig. 802) are normally plate-like with thick centres and thin margins. A central corallite is usually easily distinguished in small coralla but not in coralla >20 cm diameter. Other corallites, within the same corallum, vary greatly in shape and size. Most are inclined on the corallum surface, usually towards the periphery. There is much variation in the degree to which corallites protrude; those on even slightly convex surfaces being much more protuberant than those on concave ones. Likewise the corallite diameter and number of septa vary greatly, even between adjacent corallites. Septa are not clearly arranged in orders; major septa radiate from the columellae at regular intervals and are usually evenly exsert, up to 5 mm. The upper margins of these septa usually have 1-3 large dentations which may include a

distinct paliform crown. Costae are thick, even and have very pronounced dentations usually in the shape of pointed spines. In plate-like coralla they are arranged perpendicular to the plate margin; in others they have no regular orientation. Exothecal alveoli occur at the insertion of costae and are common in small coralla with a rapidly increasing surface area but may be uncommon, especially on the hillocky parts of coralla where costae are highly anastomosed and rarely have free inner margins. Corallite walls are primarly septothecal although secondary thickening by synapticulae may occur in protruberant corallites. Columellae are well developed, either trabecular or compact. Both endo- and exothecae are well developed, the latter sometimes forming distinct blisters.

Living colonies (Figs. 800-802) have a very wide variety of colours, browns, greens and reds being predominant with red or green oral discs.

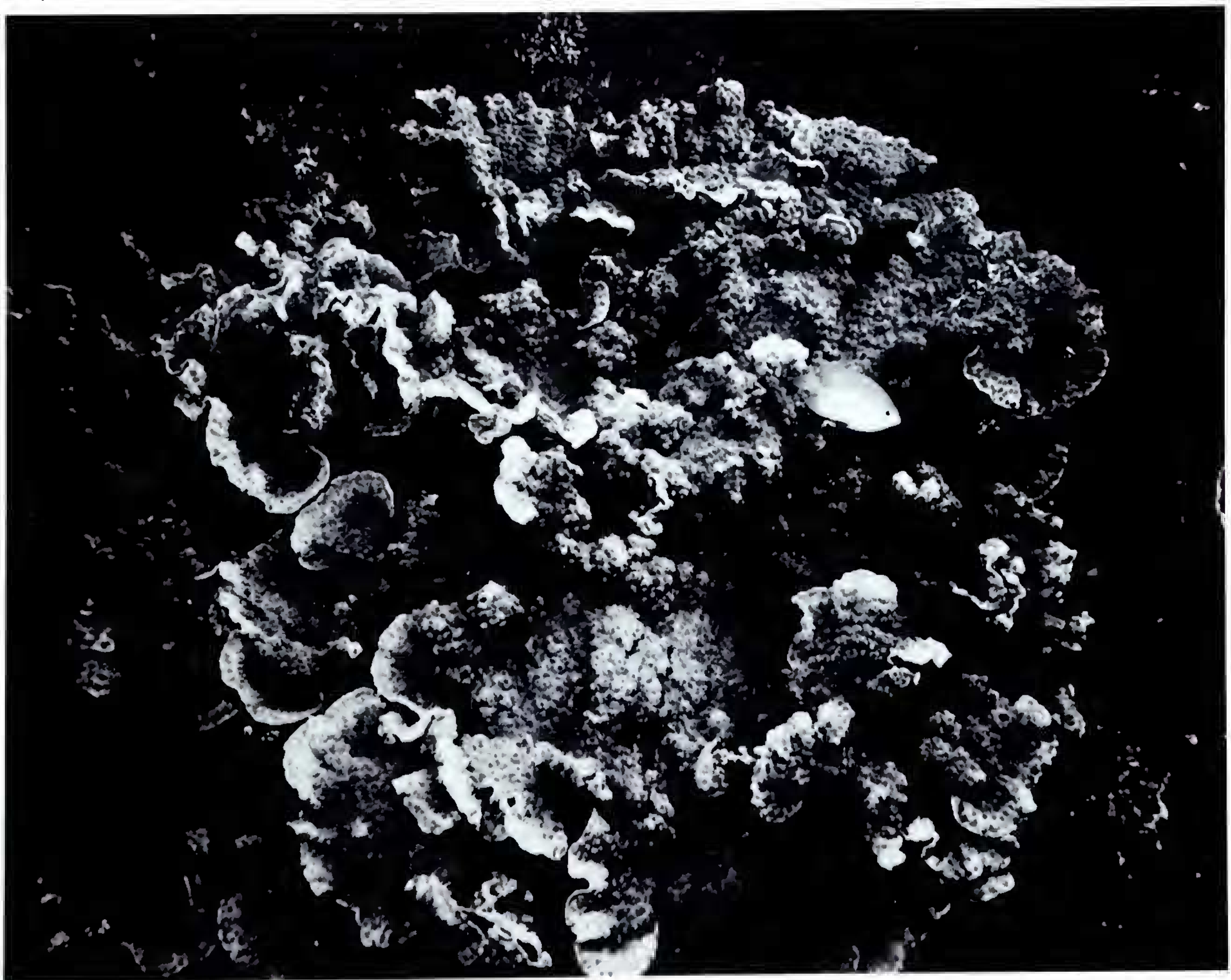
Affinities

This variable species is close to *E. orpheensis* at one extreme and *E. echinata* at the other. Differences between these species are discussed below (pp. 307 and 309).

Distribution

Many locality records attributed to this species are incorrect although it has been recorded from the Red Sea and Tuléar in the west to the Marshall Islands and Tahiti in the east.

Fig. 520 *Echinophyllia aspera* from Heron Island.



Echinophyllia orpheensis nom. nov.

Synonymy

Oxyphyllia aspera var. *tosaensis* Yabe & Eguchi, 1935a; Yabe, Sugiyama & Eguchi (1936).

Oxyphyllia aspera var. *sugiyamai* Yabe & Eguchi, 1935a; Yabe, Sugiyama & Eguchi (1936); (*pars*) Ma (1959).

Oxyphyllia aspera (Ellis & Solander); Umbgrove (1939).

Oxypora aspera (Ellis & Solander); Crossland (1952).

Echinophyllia aspera var. *sugiyamai* (Yabe & Eguchi); Pillai & Scheer (1976); ***non*** Chevalier (1975).

Echinophyllia aspera var. *tosaensis* Yabe & Eguchi, 1935a; Chevalier (1975).

Yabe *et al.* (1936) clearly illustrated this species (Pl. 36, Fig. 6, Pl. 38, Figs. 5, 6). So did Ma (1959) (Pl. 243, Fig. 1) and Umbgrove (1939) (Pl. X, Figs. 1, 2). The latter noted that in one of his specimens 'the characters of *O. aspera* var. *typica, O. aspera*

Fig. 521 *Echinophyllia aspera* from Lord Howe Island, collecting station 147, showing polyps with tentacles retracted during the day.

Figs, 522-528 *Echinophyllia orpheensis* (× 0.7).

Fig. 522 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.
Fig. 523 Holotype from Pioneer Bay, Orpheus Island, Palm Islands, collecting station 45.
Fig. 524 Paratype from Pioneer Bay, Orpheus Island, Palm Islands, collecting station 45.
Fig. 525 Paratype from Hope Island.
Fig. 526 From Bushy Island-Redbill Reef, collecting station 112.
Fig. 527 From Lizard Island, collecting station 24.
Fig. 528 From York Island, collecting station 13.

Fig. 521▼

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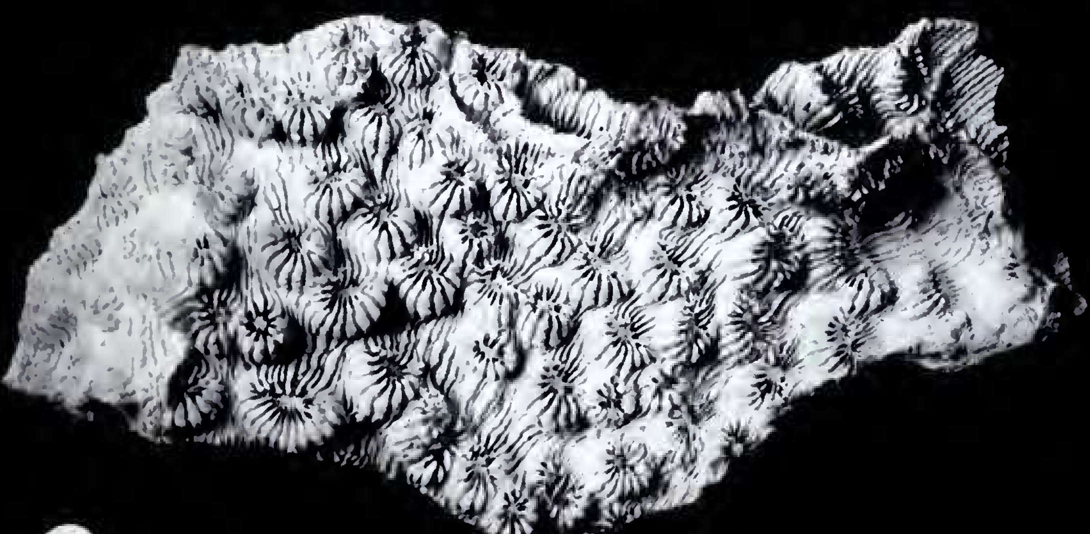

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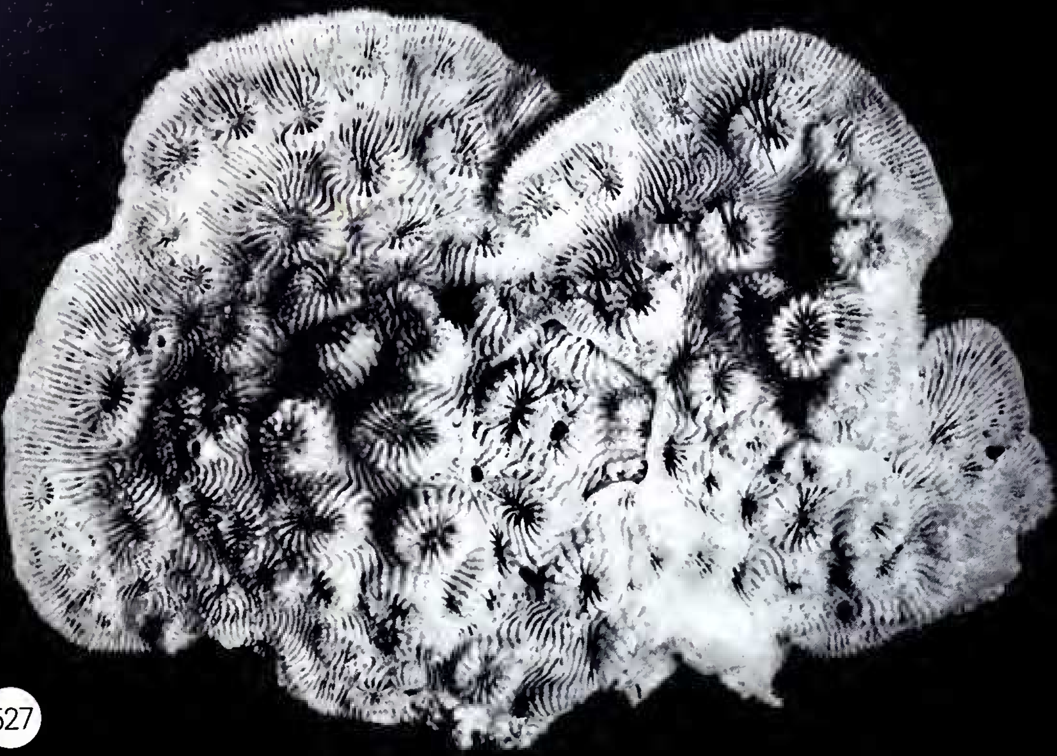

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528

var. *tosaensis* and *O. aspera* var. *sugiyamai* are combined'. Crossland recorded a specimen from the Great Barrier Reef which 'exactly resembles' Umbgrove's Fig. 2, and noted that this is 'almost certainly not the species Ellis deals with'.

Material studied

Barrier Reef NE **Murray Islands, Yorke Island** (4 specimens), **Dungeness Reef, Thursday Island, Nymph Reef, Lizard Island** (4 specimens), **Hope Island, Low Isles** (2 specimens), **Palm Islands** (51 specimens), **Whitsunday Islands** (20 specimens), **Bushy Island-Redbill Reef** (3 specimens), **Pompey Complex** (2 specimens), **Swain Reefs** (2 specimens).

These localities include collecting stations 11, 12, 13, 32, 34, 35, 39, 41, 42, 43, 45, 55, 57, 59, 69, 70, 73, 80, 87, 90, 91, 97, 98, 100, 104, 108, 112, 122, 126, 137.

Previous records from Eastern Australia

Great Barrier Reef (as *Oxypora aspera*) Crossland (1952).

Characters

Coralla are encrusting with thin, explanate margins surrounding a relatively thick, sub-massive centre. Corallites at the corallum periphery are usually inclined away from the centre with only their distal margin separated from the corallum lamina. With increasing growth the corallites become contorted cylinders radiating away from the corallum centre (Figs. 803, 804). These corallites form buds at irregular intervals with daughter corallites growing at obtuse angles. Axial corallites can be distinguished in small coralla but are usually obliterated by subsequent growth. Mature corallites may be up to 2.4 cm diameter. Septa are in two alternating orders. First order septa reach the columellae and usually have paliform lobes which may form a very distinct crown. They are evenly exsert, greatly thickened over the thecae and have very thick costae. The latter, which dominate the appearance of the corallum, are sometimes straight, sometimes undulated, but always have large dentations especially prominent near the corallite rim where they may be up to 3 mm thick. Costae of adjacent corallites are usually adjoined; if not, they end in deep alveoli. Second order septa, when present, are small, do not reach the columellae and frequently do not form costae. Columellae are always large and compact. Corallite walls are mostly septothecal. Both endothecal and exothecal thickening occurs in older corallites, the latter nearly submerging the costae in some coralla.

Living colonies may be brightly coloured, with prominently coloured costae. Most colonies, however, have cream or pale brown outer corallites or parts of corallites, with darker inner areas.

Skeletal variation

Coralla vary primarily in their degree of calcification. At one extreme (Fig. 534) septo-costae are thin and have thin, elongate dentations. Such coralla usually have little or no development of a paliform crown and columellae are relatively diffuse. At the other extreme, septo-costae are very thick and have coarse dentations. Some of this variation can occur in the same corallum with older, central corallites being more heavily calcified than younger, peripheral ones. In most coralla the latter are usually inclined on the surface of the corallum as illustrated in Fig. 526. Mature corallites are usually cylindrical with lengths up to 4.5 cm (Fig. 529) but are usually much less. There appears to be no correlation between the degree of calcification and the length of mature corallites.

Colonies of *E. orpheensis* seldom attain a diameter of 40 cm and none have been seen to form large, flat plates as have other *Echinophyllia* species. This species does not normally occur under ledges or overhangs as do other *Echinophyllia*.


Fig. 529 ▲


Fig. 530 ▲


Fig. 531 ▲

Fig. 533 ▼

Fig. 534 ▼


Fig. 532 ▲

Affinities

As noted above this species considerably increases the diversity of forms included in the genus *Echinophyllia.* It differs from all other *Echinophyllia* in the development of protruding, branching corallites, also in the development of the costae. Despite the confusion of earlier authors, it is readily distinguished from *E. aspera* by these characters, by the development of a paliform crown and also by the growth form which is much more massive than normally observed in *E. aspera.*

Inclusion of *E. orpheensis* in *Echinophyllia* is clear and it shows no close affinity with any other genus. It may be noted that the development of the costae and paliform lobes gives this species a curious but superficial resemblance to the holotype of *Bikiniastrea laddi* Wells.

Etymology

Named after Orpheus Island from where much research for the present study was based.

Holotype (Fig. 539)

Dimensions: The maximum dimension is 14.7 cm.

Locality: South Pioneer Bay, Orpheus Island, Palm Islands, collecting station 91.

Depth: 10 m.

Collector: J.E.N. Veron.

Holotype: British Museum (Natural History).

Paratypes (Figs. 540, 541)

Fig. 540. Queensland Museum, Australia.

Fig. 541. Australian Institute of Marine Science.

Distribution

This species is known to occur in Japan and the Bonin Is. (Yabe *et al.*, 1936), the Philippines (a specimen in the United States National Museum), Indonesia (Umbgrove, 1939), and the Great Barrier Reef.

Echinophyllia echinata (Saville-Kent, 1871)

Synonymy

Tridacophyllia echinata Saville-Kent, 1871.

? *Echinopora magna* Gardiner, 1904.

Echinophyllia echinata (Saville-Kent); Chevalier (1975).

? *Physophyllia ayleni* (Wells); *sensu* Pillai & Scheer (1976).

As noted by Chevalier, the holotype of *Tridacophyllia echinata* Saville-Kent, a small, immature corallum from the Solomon Islands, belongs to this species.

Figs. 529-534 *Echinophyllia orpheensis* (× 5.0).

Fig. 529 From Butterfly Bay, Hook Island, same corallum as Fig. 522.
Fig. 530 From Pioneer Bay, Orpheus Island, same corallum as Fig. 524.
Fig. 531 From Hope Island, same corallum as Fig. 525.
Fig. 532 From Wistari Reef, same corallum as Fig. 526.
Fig. 533 From Lizard Island, same corallum as Fig. 527.
Fig. 534 From Yorke Island, same corallum as Fig. 528.

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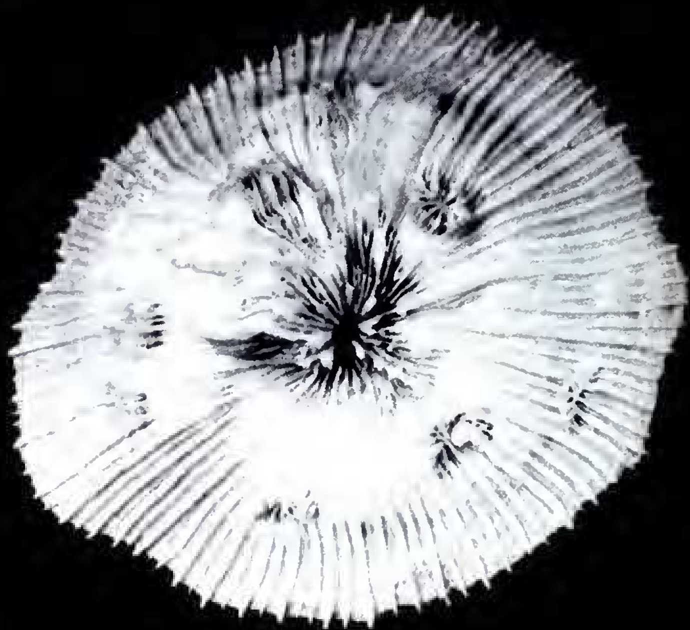

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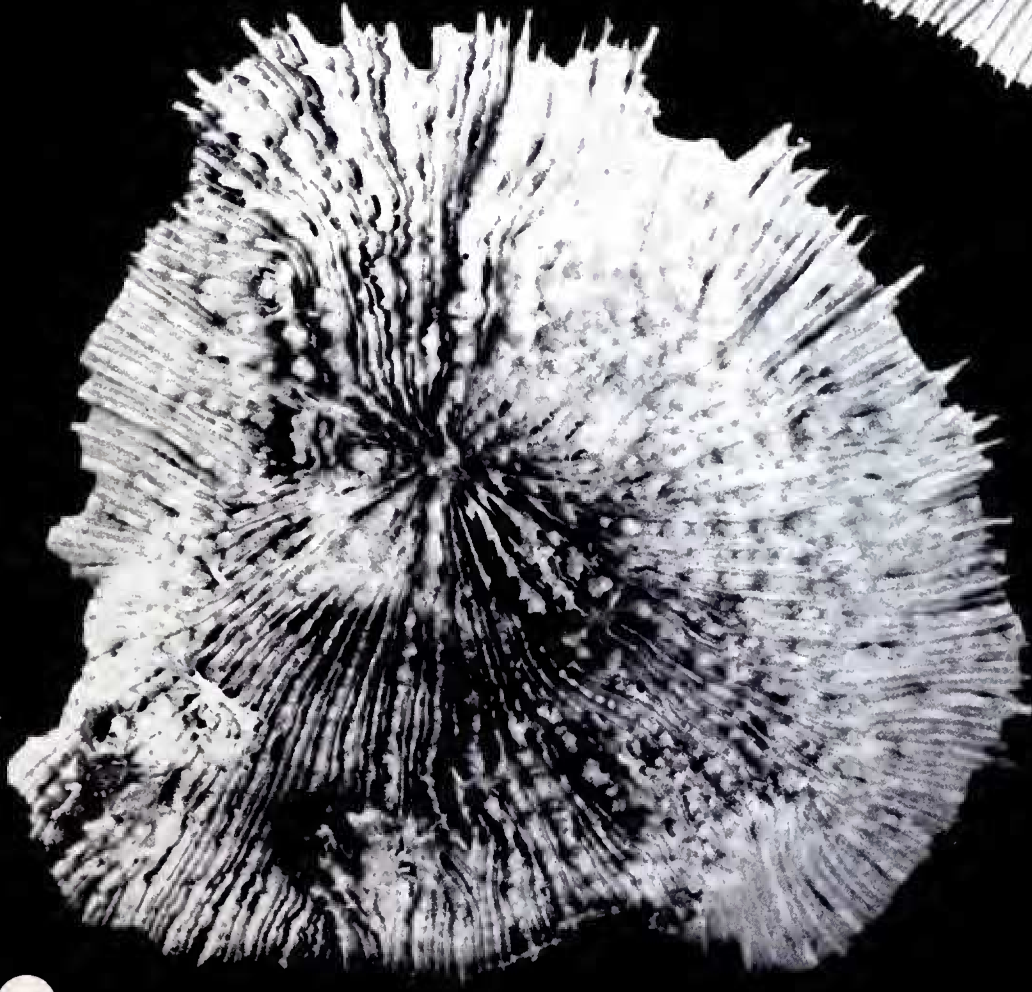


537

Material studied

Big Mary Reef, Yorke Island (5 specimens), **Murray Islands** (3 specimens), **Ashmore Reef** (2 specimens).

These localities include collecting stations 28, 107, 125, 126, 130, 131.

Previous records from Eastern Australia

Not previously recorded.

Characters

All coralla of the present series are thin, mostly flat plates. All have very large conspicuous central corallites from which all major costal ridges radiate. Up to six orders of septa may occur in the central corallite of large colonies. These are often arranged in hexameral cycles. Those of first two orders (or cycles) are thicker (<1.5 mm) and more exsert than those of higher orders and some may develop large paliform lobes. All have 1-3 large, lobed, dentations. The first 3 or 4 orders of septa usually reach the columellae, the remainder usually have free or anastomosed inner margins at increasing distances from the columellae and usually have several fine, elongate dentations. In some coralla, all septa reach the columellae. The latter are always very large (up to 6 mm diameter) and compact. Secondary corallites are shallow or superficial and are widely and irregularly spaced. They are usually elliptical and may be inclined towards the corallum margins. Two to four orders of septa can usually be distinguished. Those of the first order are much thicker and more exsert than the others and usually have a single paliform dentation which may be very high. Columellae of secondary corallites may be compact or composed of only a few trabeculae.

The arrangement and appearance of the costae is usually distinctive. They all radiate from the central corallite. They vary greatly in height (<2.5 mm) and width (<2.5 mm) according to their original order. The ornamentation of the costae varies greatly in different coralla; some are nearly glabrous, others have acute dentations, frequently with fine spinules or granules at their tips. Deep alveoli usually occur at the point of insertion of new costae. Large, vesicular endothecal dissepiments are developed towards the centre of large colonies and frequently the coenosteum is blistered.

The only recorded colours of this rare species are uniform browns and greens (Fig. 805).

Affinities

The present series, which is unlikely to represent the full variability of the species, is closest to some growth forms of the much more common *E. aspera*. As far as is known it does not form the thick plates or sub-massive forms that are common in *E. aspera*. It is primarily distinguished from thin, explanate plates of *E. aspera* by the characters of the large central corallite, especially the very prominent first and second order septo-costae. Secondary corallites resemble those of *Oxypora lacera* more than *E. aspera* in being shallow and elliptical rather than protuberant and radially symmetrical as is usually the case with *E. aspera*.

Figs. 535-538 *Echinophyllia echinata*, Figs 536-538 (× 1.0).

Fig. 535 From Dewar Island, Murray Islands, collecting station 88 (× 0.5).
Fig. 536 From Big Mary Reef, collecting station 131.
Fig. 537 From Ashmore Reef, collecting station 107.
Fig. 538 From Yorke Island, collecting station 126.

Distribution

Confirmed reports of *E. echinata* are all from the western Pacific; the Solomon Islands, New Caledonia and the Great Barrier Reef. However, it appears to have been recorded twice from the Maldive Islands (by Gardiner, 1904 and Pillai & Scheer, 1976; see synonymy above).

Echinophyllia echinoporoides n. sp.

Material studied

Pearce Cay (3 specimens), **Yorke Island** (4 specimens), **Lizard Island** (3 specimens), **Palm Islands** (2 specimens), **Whitsunday Islands** (14 specimens).

These localities include collecting stations 11, 39, 55, 96, 97, 98, 124, 125.

Previous records from Eastern Australia

Not previously recorded.

Characters

All coralla of the present series are explanate plates with thin edges and a central area up to 3 cm thick, the latter frequently formed by successive overgrowths. Mature corallites are irregularly distributed. They are usually more widely separated in the direction of the costae, those of the same age sometimes forming irregular, concentric rows. Most mature corallites are plocoid or sub-plocoid; none protrude more than 2.5 mm. Mature calices average 3.4 mm diameter and are circular in outline except towards the corallum periphery where their shape may be irregular. No central corallite can be distinguished in the present series. Septa are in two alternating orders. Second order septa are frequently absent but are usually reduced to a few spines on the theca. Second order costae, if present, are very reduced. First order septa, 7-13 in

Fig. 538 ▼

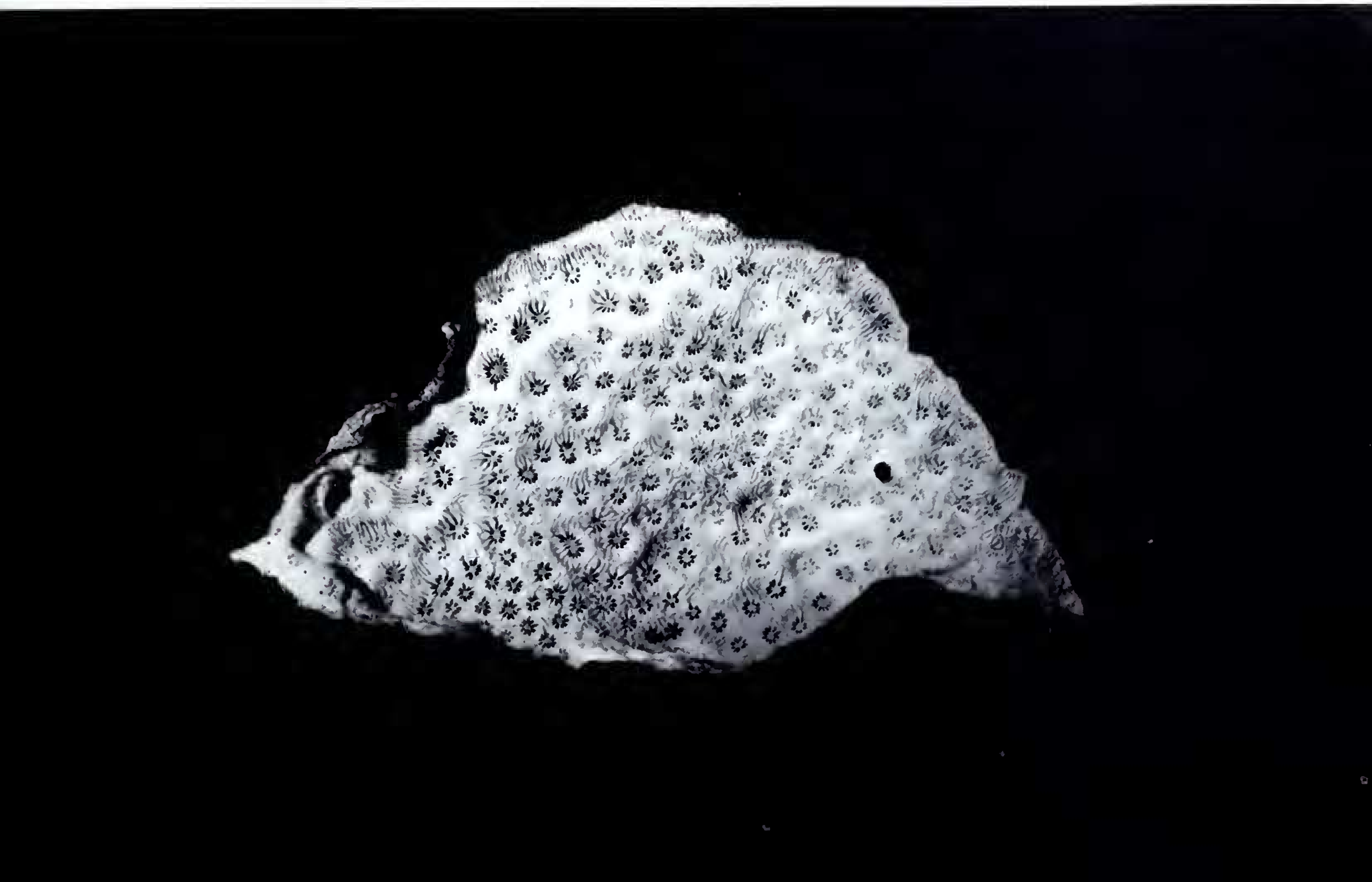
number, extend inwards horizontally almost to the columellae. They have 1-4 tall paliform dentations, the innermost of which slant towards the columellae. The latter are compact, although their formation from dentations of the vertical, inner septal margins, can usually be seen. The sides of the septa are finely granulated. In some coralla the costae radiate from the corallum centre and are perpendicular to the margins. In others, especially at the centre of relatively thick coralla, they radiate from the corallites in all directions, become adjoined in an irregular manner and are frequently sinuous or crenellated. The costae are always finely dentate, the dentations varying in appearance from spines to beads. Small alveoli are present at the insertion of the costae but are seldom abundant. On their undersurface, all coralla are finely costate, the costae being glabrous or minutely dentate. The walls are primarily septothecal. Exothecal dissepiments are conspicuous towards the centre of most coralla.

This species is uncommon on the Great Barrier Reef. Colonies have a wide range of colours, from cream to dark brown-green, which are mostly uniform across the colony (Fig. 806).

Skeletal variation

As with other *Echinophyllia* species, most skeletal variation is attributable to growth states of the corallites and to their degree of calcification. Where calcification is minimal, costae are thin and straight and costal dentations spinulose. Thecae are mostly indistinguishable. Where it is maximal, thick septothecal walls are formed and the costae are thick and usually sinuous.

Fig. 539 Holotype of *Echinophyllia echinoporoides* from Cateran Bay, Border Island, Whitsunday Islands, collecting station 96 (× 0.7).



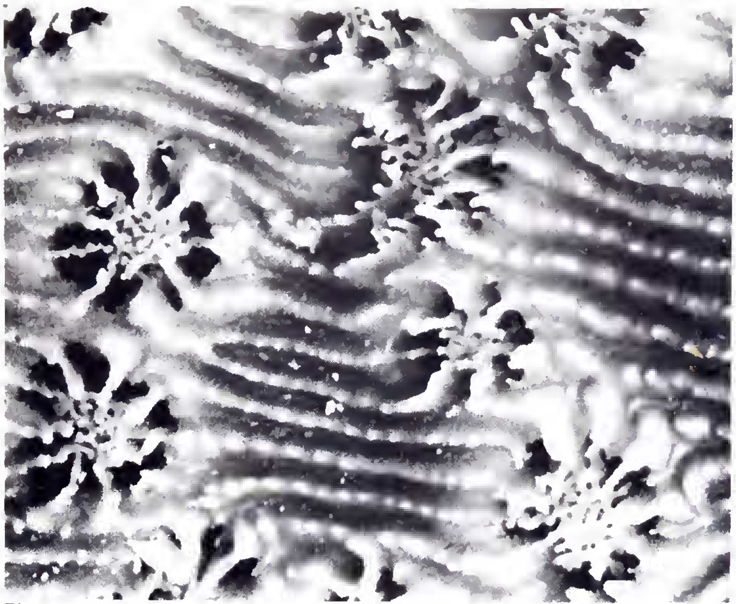
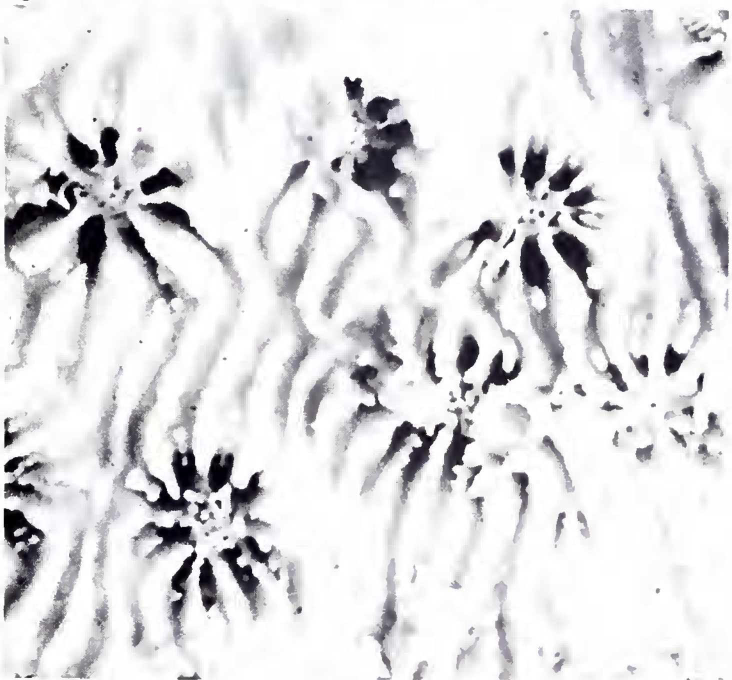


Fig. 540 ▲

Fig. 541 ▲



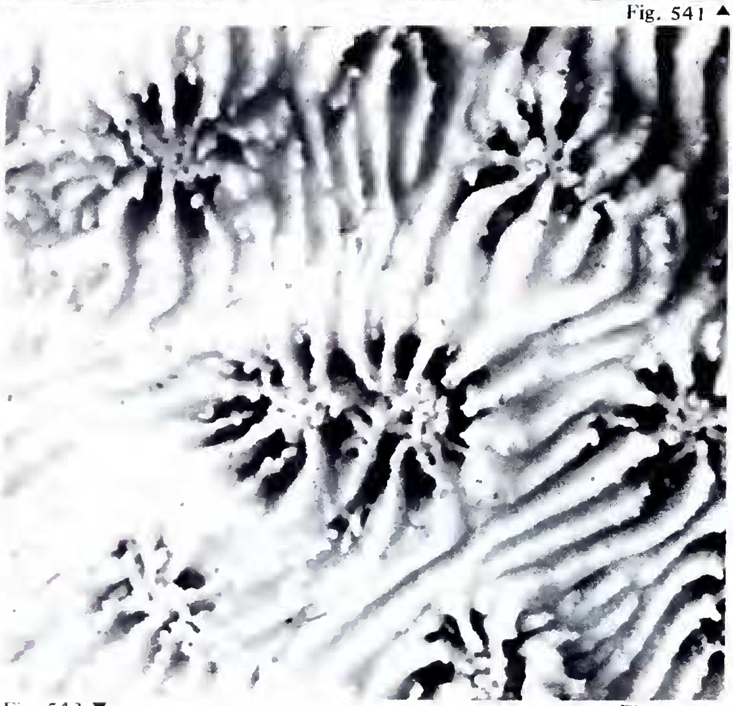
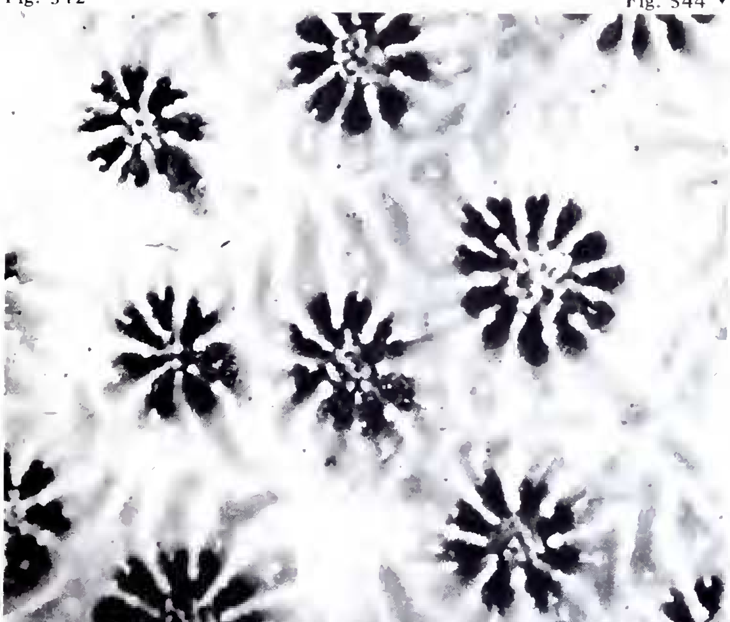


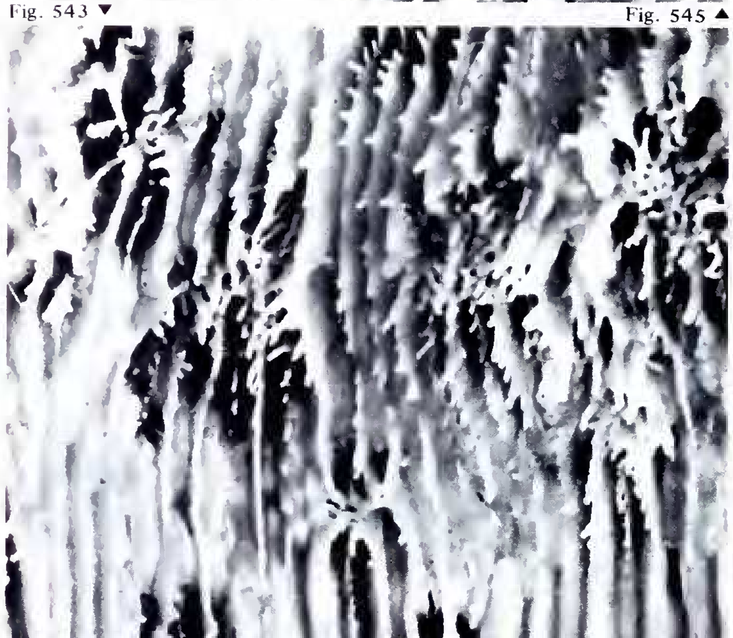
Fig. 542 ▲

Fig. 544 ▼

Fig. 543 ▼

Fig. 545 ▲





Affinities

Echinophyllia echinoporoides does not closely resemble any other *Echinophyllia* although it clearly belongs in this genus. It has some characters normally found in *Oxypora* but the well defined, circular corallites and lack of alveolar perforations are very different from those of *O. lacera.*

There is a superficial resemblance between this species and *Echinopora lamellosa* (Esper) (Family Faviidae) which has a similar growth form and corallites of similar shape, size and density. However, although these two genera were confused by some early authors (see p. 297), both clearly exhibit the characters of their respective families and the present species is distinguishable even underwater by its costae and alveoli.

Etymology

Named because of the close resemblance between this species and *Echinopora lamellosa.*

Holotype (Fig. 539)

Dimensions: The maximum dimension is 13.5 cm.

Locality: Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.

Depth: 5 m.

Collector: M. Pichon.

Holotype: British Museum (Natural History).

Paratypes

Queensland Museum, Australia.

Australian Institute of Marine Science.

Distribution

Echinophyllia echinoporoides is only known from the Great Barrier Reef and the Celebes.

GENUS *OXYPORA* SAVILLE-KENT, 1871

Generic synonymy

Trachypora Verrill, 1864.

Oxypora Saville-Kent, 1871; Yabe & Eguchi (1935b); Wells (1936); Vaughan & Wells (1943); Crossland (1952); Wells (1956).

Saville-Kent created the genus *Oxypora* to replace *Trachypora* Verrill, which had been used by Edwards & Haime for a fossil genus of Cyathophyllidae.

Type species *Trachypora lacera* Verrill, 1864 by subsequent designation (Wells, 1936b).

Two species, *O. lacera* Verrill and *O. aspera* Verrill (*non* Ellis & Solander) were attributed to this genus by Saville-Kent and three species, *O. lacera, O. contorta* and an unnamed species by Yabe & Eguchi (1935b). The latter authors

Figs. 540-545 *Echinophyllia echinoporoides* (× 5.0).

Fig. 540	Paratype, from Lizard Island.
Fig. 541	Paratype, from Orpheus Island, Palm Islands, collecting station 55.
Fig. 542-544	From Cateran Bay, Long Island, Whitsunday Islands, collecting station 96; Fig. 542, the holotype, same corallum as Fig. 539.
Fig. 545	From Hook Island, Whitsunday Islands, collecting station 39.

placed *Oxypora* in a new family, Oxyporiidae, noting that 'its systematic position may be near Echinoporidae and Tridacophyllidae, in the Imperforata'. Yabe *et al.* (1936) recognised two species, *O. lacera* and *O. titizimaensis*, the latter a new name for the *O. contorta* of Yabe & Sugiyama (1935a). Since then, only one species has been added to the genus, *O. glabra* Nemenzo.

Of the above species, *O. aspera* Ellis & Solander is the type species of *Echinophyllia.* However, Yabe & Sugiyama (1935a) also made it the genotype of their new *Oxyphyllia*, a monospecific genus automatically invalidated by the priority of *Echinophyllia* (p. 297). *Oxypora contorta* (Quelch, not Yabe & Sugiyama), was described from a single specimen from Ambon (Indonesia) and Ma (1959) listed a second specimen of the species from Palau. Despite Quelch's comment that 'this species is close to *Oxypora lacera* Verrill, but can easily be distinguished, among other characters, by the arrangement and structure of the calices' it appears probable that it is not a distinct species. Neither can *O. titizimaensis* be maintained as a separate species. The three specimens attributed to this species are identical to some *O. lacera* of the present series collected from very sheltered biotopes. *Oxypora glabra* Nemenzo remains as a second, valid, species of *Oxypora.*

Oxypora lacera (Verrill, 1864)

Synonymy

Trachypora lacera Verrill, 1864; Duncan (1884).

Oxypora contorta Quelch, 1886.

Echinophyllia lacera (Verrill); Gardiner, 1904.

Oxypora lacera (Verrill); Yabe & Eguchi (1935b); Yabe, Sugiyama & Eguchi (1936); Umbgrove (1939); Crossland (1952); Wells (1954); Rossi (1954); Stephenson & Wells (1955); Searle (1956); Ma (1959); Nemenzo (1959); Pichon (1964); Chevalier (1975).

? Echinophyllia rugosa Chevalier, 1975.

Oxypora titizimaensis Yabe, Sugiyama & Eguchi, 1936.

Oxypora contorta was placed in synonymy with *O. lacera* by Wells (1936b), Yabe *et al.* (1936), Eguchi (1938) and subsequent authors.

The holotype of *O. titizimaensis* is a piece from the edge of a thin, highly perforate corallum. It is identical to specimens in the present series collected from protected, poorly illuminated biotopes.

Echinophyllia rugosa Chevalier, known and described from a single small specimen, does not appear to differ from heavily calcified parts of *O. lacera* coralla as described below.

Material studied

Bramble Cay (3 specimens), **Anchor Cay** (3 specimens), **Campbell Islet, Darnley Island** (3 specimens), **Big Mary Reef** (3 specimens), **Yorke Island** (17 specimens), **Warrior Reef** (5 specimens), **Murray Islands** (12 specimens), **Dungeness Reef** (2 specimens), **Ashmore Reef, Thursday Island, Wai Weer Island, Tijou Reef** (3

Figs. 546-551 *Oxypora lacera*, Figs. 546, 548, 550 (× 2.5), Figs. 547, 549, 551 (× 5.0).

Figs. 546, 547 From Frigate Cay, Swain Reefs, collecting station 81.
Figs. 548, 549 From Pioneer Bay, Orpheus Island, Palm Islands, collecting station 91.
Figs. 550, 551 From between Orpheus and Fantome Island, Palm Islands, collecting station 60.

Fig. 546 ▲

Fig. 547 ▲

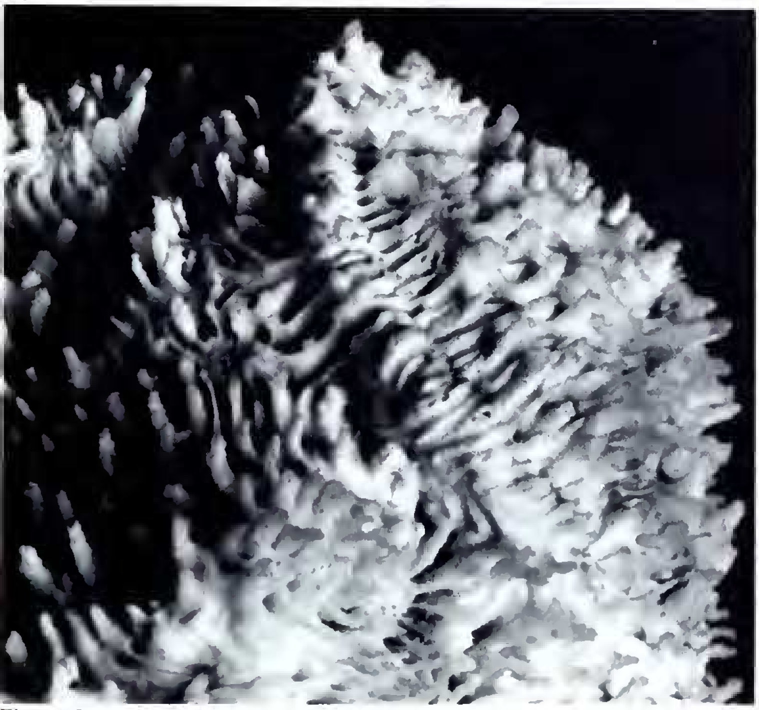


Fig. 548 ▲

Fig. 549 ▲

Fig. 550 ▼

Fig. 551 ▼

specimens), **Bewick Island, Lizard Island, Eyrie Reef, Hope Island, Low Isles** (2 specimens), **Palm Island** (22 specimens), **Whitsunday Island** (12 specimens), **Bushy Island-Redbill Reef, Pompey Complex** (3 specimens), **Frigate Cay** (3 specimens), **Swain Reefs** (2 specimens).

These localities include collecting stations 2, 8, 13, 18, 19, 27, 28, 29, 30, 34, 37, 39, 42, 43, 55, 56, 58, 60, 69, 71, 80, 81, 91, 97, 98, 105, 107, 110, 120, 122, 123, 125, 126, 128, 129, 131, 132, 135, 137.

Previous records from Eastern Australia

Low Isles, Stephenson & Wells (1955); **South Molle Island**, Stephenson & Wells (1955). Crossland (1952) discusses three specimens from the Great Barrier Reef but gives no definite localities.

Characters

Coralla usually form thin, explanate laminae or overlapping laminae loosely attached to the substrate at the oldest part (Figs. 558, 807, 808). Sometimes coralla are loosely encrusting and consequently have irregular surfaces which may develop into one or more low, irregular, hollow columns. Corallites have a very wide variety of forms depending on their age and degree of calcification. With very rare exceptions they are bilaterally symmetrical and not inclined on the corallum surface. They are usually elliptical in outline, the longer axes being arranged concentrically. Septo-costae are arranged in two alternating orders, the second of which is abortive. First order septa are fused with the columellae. They mostly consist of one (rarely more) high dentation which frequently has an irregularly serrated upper margin. Small, irregular dentations are sometimes present on the inner septal margins which are usually fused with the columellae. The latter may be large and spongy, small and fused or, sometimes, absent. Septa are usually thickened in the position of the theca which takes the form of a rudimentary septotheca in some coralla but is usually absent. Costae are usually thick and straight and are normally perpendicular to the corallum margin. In some coralla, two alternating orders can be distinguished. All costae are ornamented with irregular dentations which have a very wide variety of shapes and sometimes have clusters of spinules at their tips. Deep alveoli are present at the insertion of all costae, the inner and upper margins of which are irregularly dentate. Sometimes the alveoli penetrate to the undersurface of the corallum. These are not the same as the slit-like pores between the costae of thin laminae. The latter, although present at the periphery of most coralla, are not diagnostic of *Oxypora* and may be absent in heavily calcified specimens. The undersurfaces of coralla are costate, the costae being heavily ornamented with dentations and spinules which frequently branch.

Living colonies (Figs. 809, 810) are usually brown, green or reddish in colour. Colours are either uniform throughout whole colonies with individual corallites relatively indistinct or else oral discs are red or green. When polyps are expanded at night the whole colony surface becomes covered with fine tentacles and individual polyps cannot be recognised.

Figs. 552-557 *Oxypora lacera* (× 5.0).

Fig. 552 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.
Fig. 553 From York Island, collecting station 13.
Fig. 554 From Darnley Island, collecting station 31.
Fig. 555 From Bushy Island-Redbill Reef, collecting station 80.
Fig. 556 From Low Isles.
Fig. 557 From the Pompey Complex, collecting station 105.

Fig. 558 *Oxypora lacera* at Heron Island with tentacles retracted during the day.

Fig. 552 ▲

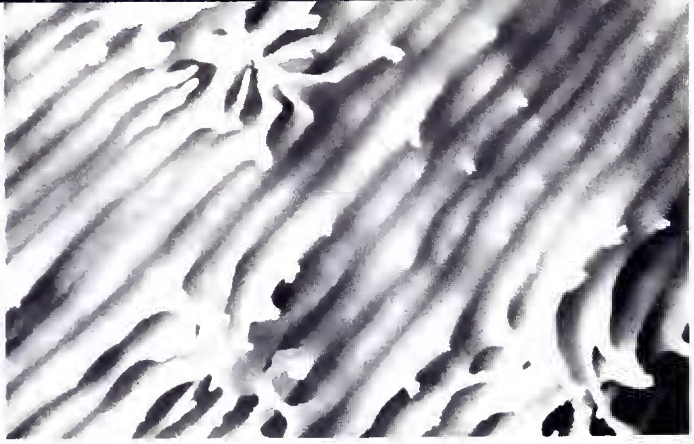


Fig. 553 ▲

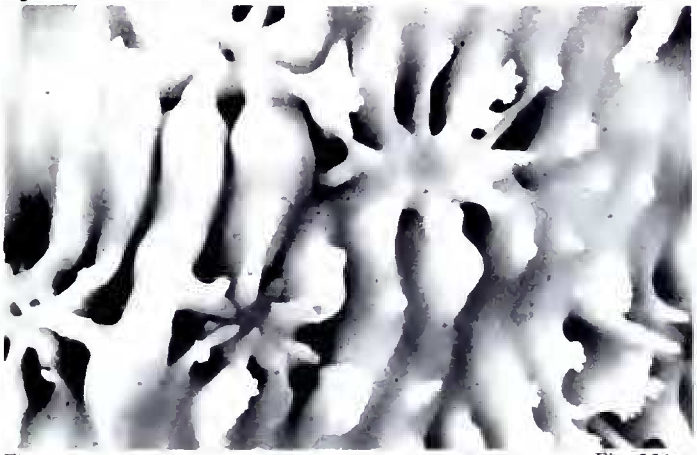


Fig. 554 ▲

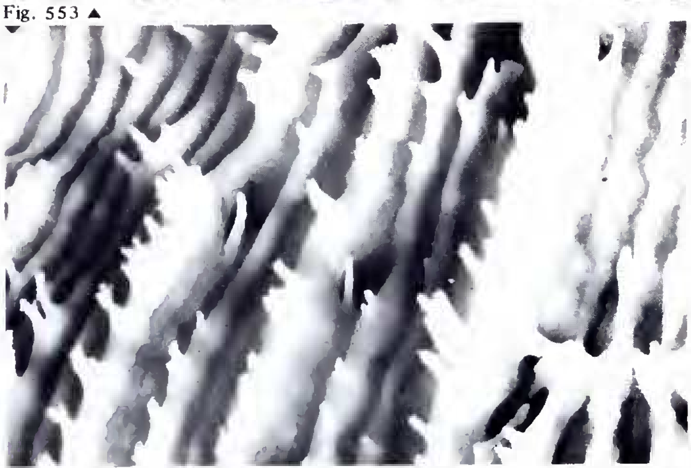


Fig. 555 ▲

Fig. 556 ▼

Fig. 557 ▼

Fig. 558 ▼

Skeletal variation

Oxypora lacera has a very wide range of variation in all skeletal characters. The older, central parts of coralla, especially when attached to a substrate, are usually very dissimilar from the fine peripheral parts and, as with several *Echinophyllia* species, there is wide variation in the degree to which different coralla are calcified. Figures 548-557 illustrate most of the range of variation in the present series.

Oxypora lacera from protected biotopes (Figs. 552-556)

This species frequently occurs in deep water under protective ledges or at the mouth of caverns etc. where it forms very thin, delicate, explanate plates. Corallites near the periphery of these plates have few septa. They mostly consist of small, loosely trabecular columellae encircled by a crown of septal dentations. The costae are usually fine, widely spaced and frequently separated by the slit-like pores noted above. Older, more heavily calcified parts of these coralla usually have a well defined central corallite and regularly radiating costae.

Oxypora lacera from partly exposed biotopes (Figs. 546-551)

Coralla from shallow reef biotopes are much more variable. Corallites are relatively closely compacted and may be very dissimilar. Septa may be grossly thickened (up to 4 mm) and have long, branching dentations (Fig. 547).

Affinities

There is a very close resemblance between *O. lacera* and *O. glabra*. The latter has similar alveoli, intercostal slits, and corallites of similar size. In both species the corallites show little or no inclination towards the corallum periphery. The primary differences between the two are the lack of costal ornamentation in *O. glabra*, the reduction of the columellae and the fusion of the inner septal margins.

Oxypora species are reliably distinguished from *Mycedium* by the inclination of the corallites and the complete absence of alveoli in the latter. In the present series the two cannot be confused, although both Wells (1954) and Chevalier (1975) have emphasised their close affinity. *Oxypora* species are less readily distinguished from *Echinophyllia, O. lacera* and *E. aspera* being particularly close. The latter usually have slightly inclined corallites near the periphery and usually have radially symmetrical corallites near the corallum centre, the reverse of the usual situation with *O. lacera*. There are no intercostal slits in any of the present series of *Echinophyllia* although these are usually also absent from the central parts of *O. lacera* coralla. *Echinophyllia aspera* usually has more than 12 primary septa; *O. lacera* usually has less than 12.

Distribution

Widely distributed from the Red Sea and western Indian Ocean east to the Marshall Islands, New Caledonia and the Loyalty Islands.

Oxypora glabra Nemenzo, 1959

Synonymy

Oxypora glabra Nemenzo, 1959.

Echinophyllia glabra (Nemenzo); Chevalier (1975).

Material studied

Yorke Island, Murray Island, Lizard Island, Palm Islands.
These localities include collecting stations 29, 35, 125.

Previous records from Eastern Australia

Not previously recorded.

Characters

Only two specimens of this species have previously been described: the holotype from the Philippines and a specimen from New Caledonia recorded by Chevalier. The latter specimen differs from the type in having better developed columellae and a more regular arrangement of the costae, but otherwise they are similar. Of the present specimens, one (Fig. 559) is similar to the type, another is close to Chevalier's specimen. All are flat, explanate coralla with corallites irregularly distributed and of very irregular size (5-8 mm diameter). Most corallites have 4-8 septa of varying size which extend to the corallite centre, usually in a clockwise spiral. Septa have 1-3 high septal spines and mostly fused inner margins. There is almost no development of columellae. Costae are equal and mostly perpendicular to the corallum margins. Very large alveoli occur at the insertion of costae or septo-costae. The latter case applies to the inner margins of all septa that are not fused or do not reach the centre of the corallite. Such intratentacular alveoli are not distinguishable from the others and have the general appearance of deep interseptal loculi. Otherwise there are no interseptal loculi, the corallites being entirely superficial. Sometimes exothecal alveoli are arranged in rows. Usually there is a high spine or series of dentations on each costa at its insertion and there is no clear distinction between these and the most simple corallites containing a very small number of septa. Intercostal pores are developed only at the corallum margins. There is no evidence of the formation of any kind of theca and little development of exothecal dissepiments. Most of the corallum is costate. The undersurface is costate, the costae having no ornamentation.

The only recorded colour of living colonies is dark brown.

Affinities

This species is returned to genus *Oxypora* after having been placed in *Echinophyllia* by Chevalier (1975). The presence of intercostal pores and the lack of thecae indicate a close affinity with *Oxypora lacera.*

Distribution

Oxypora glabra is known only from the Philippines, New Caledonia and the northern Great Barrier Reef.

GENUS *MYCEDIUM* OKEN, 1815

Generic synonymy

Mycedium (*pars*) Oken, 1815; (*pars*) Edwards & Haime (1860); Verrill (1901); Vaughan & Wells (1943); Wells (1956).

Phyllastraea Dana, 1846.

Type species *Mycedium elephantotus* Pallas, 1766.

Wells (1955b) commented that *M. tubifex* (Dana) from Moreton Bay displays 'such wide variation from thin, widely spaced, to close, thick, irregularly and spinosely dentate septa, and from superficial through pocket-shaped to irregularly elevated, cylindrical calices, as to make it probable that the various "species" of this genus, *M. elephantotus* (Pallas) (*M. okeni* Matthai), *M. explanatum* Verrill, *M. tenuicostatum* Verrill and *M. tubifex* (Dana) (*M. aspera* Matthai), are actually a single variable species'. This view was supported by Chevalier (1975) and is also the conclusion of the present study.

Characters

Mycedium is like *Echinophyllia* but forms folia which are flat or sometimes contorted with protuberant, nariform, outwardly inclined calices. Pits at the insertion of the costae are absent.

Mycedium elephantotus (Pallas, 1766)

Synonymy

Madrepora elephantotus Pallas, 1766.

Mycedium elephantotus (Pallas); Yabe & Eguchi (1935b); Yabe, Sugiyama & Eguchi (1936); Ma (1937, 1959); Eguchi (1938); Umbgrove (1940); Rossi (1954); Nemenzo (1959); Pichon (1964); Scheer (1972); Chevalier (1975).

Phyllastraea tubifex Dana, 1846; Verrill (1864).

Mycedium okeni Edwards & Haime, 1851a; Edwards & Haime (1860); Matthai (1924).

Mycedium tubifex (Dana); Edwards & Haime (1860); Rehberg (1892); Yabe & Eguchi (1935b); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Wells (1955b); Stephenson & Wells (1955); Searle (1956); Ma (1959); Scheer & Pillai (1974).

Mycedium explanatum (Verrill); Verrill (1901); Ma (1959).

Mycedium tenuicostatum Verrill, 1901; Yabe & Eguchi (1935b); Yabe, Sugiyama & Eguchi (1936); Eguchi (1938); Ma (1959).

Mycedium aspera (Ellis & Solander); *sensu* Matthai (1924); Yabe & Sugiyama (1935a).

Material studied

Bramble Cay (2 specimens), **Anchor Cay** (2 specimens), **Big Mary Reef, Yorke Island** (5 specimens), **Murray Island** (7 specimens), **Aureed Island, Dungeness Reef, Tijou Reef** (5 specimens), **Lizard Island** (3 specimens), **Hope Island, Low Isles** (4 specimens), **Palm Islands** (42 specimens), **Bowden Reef, Gould Reef, Parker Reef, Whitsunday Islands** (12 specimens), **Bushy Island-Redbill Reef** (9 specimens), **Pompey Complex** (2 specimens), **Frigate Cay** (4 specimens), **Swain Reefs** (6 specimens), **Heron Island, Lord Howe Island** (8 specimens).

These localities include collecting stations 2, 8, 13, 27, 28, 29, 30, 32, 33, 34, 35, 36, 37, 38, 39, 42, 45, 55, 56, 57, 58, 60, 69, 75, 76, 79, 80, 81, 90, 97, 98, 102, 103, 112, 114, 122, 125, 128, 129, 131, 133, 140, 143.

Previous records from Eastern Australia

Low Isles (as *M. tubifex*) Stephenson & Wells (1955); **Moreton Bay** (as *M. tubifex*) Wells (1955b), Lovell (1975); **Lord Howe Island,** Veron & Done (1979).

Characters

Colonies form large plates or series of plates loosely encrusting the substrate. They usually grow horizontally but are often found under overhangs where they form nearly vertical sheets up to 3 m across. Most colonies have an easily recognised central corallite usually near the centre of horizontal laminae or near the upper edge of inclined ones. Corallites sometimes form concentric circles but are usually irregularly distributed. They are usually inclined on the surface of the corallum facing away from the central corallite. In most coralla, only their distal wall projects from the corallum surface. Some corallites, however, may be cylindrical and have irregularly distributed lateral buds. Almost all corallites have a much greater diameter at their outer perimeters than at their bases.

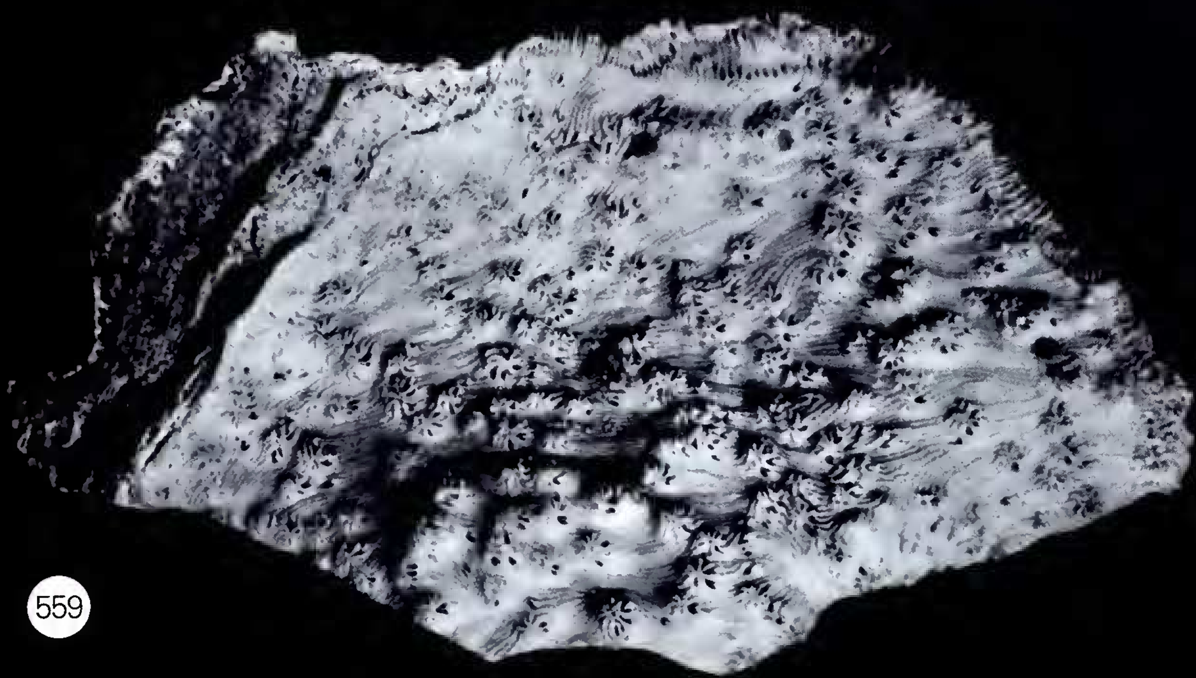
Three orders of septa can usually be recognised. Third order septa are very fine and do not form costae. Second order septa are thinner than those of the first order and may form thin costae alternating with first order septo-costae. First order septa are usually irregularly exsert. First order costae may be regular to very irregular in size and shape and have varying ornamentations. With few exceptions they have finely

serrated margins and most have lobed dentations. Fine serrations are usually prominent on the dentations and in some coralla occur as clusters of tiny, sometimes branching spinules. Dentations are especially prominent on costae at the distal side of corallites where they may attain lengths up to 1 cm. In many coralla, however, dentations are no more than low ridges or thickenings of the costae. The columellae are likewise very variable. In some coralla they consist of a few twisted septal dentations, in others they are large and compact. In most coralla the walls are primarily septothecal, especially towards the corallum centre. At their periphery they

Figs. 559, 560 *Oxypora glabra* (× 0.6).

Fig. 559 From Bullumbooroo Bay, Great Palm Island, collecting station 35, showing close similarity with the holotype.

Fig. 560 From Lizard Island.



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become increasingly trabeculo-septothecal. There is little or no evidence of endotheca. Vesicular exothecal dissepiments usually make up a large component of the corallum centre but are usually absent from the periphery.

Living colonies (Figs. 811-813) have a very wide range of colours which adds further to their variable appearance underwater. Some are uniform in colour, usually brown, grey, pink or green. Some have a different colour around the colony perimeter. Many have brightly coloured oral discs, usually green or red.

Skeletal variation

As suggested by its synonymy, *M. elephantotus* throughout the Indo-Pacific has a very wide range of variation and much of this is found in a single general locality (e.g. Wells' comments on *Mycedium* from Moreton Bay p. 318). This variation appears to have a largely genotypic origin, so that even adjacent colonies can show marked skeletal differences, especially in the size of the corallites. The mean horizontal diameter of mature corallites including costae ranges from 0.9-1.9 cm in different coralla of the present series. Costae are also very variable in their ornamentation (as noted above) but there is no apparent correlation between the development of ornamentation and the size of the corallites.

A single distinctive ecomorph can be recognised in colonies growing as thin, flat sheets under overhangs or ledges. Such colonies have strongly inclined corallites of intermediate size (averaging 1-1.4 cm diameter). Their distal walls are usually vase-shaped, with narrow bases. Their costae are moderately ornamented, with a lesser degree of ornamentation appearing to occur where tidal currents are evident.

Coralla from reef biotopes exposed to strong illumination are relatively heavily calcified. Corallites usually have thick septothecal walls and may be cylindrical in shape towards the corallum centre.

Affinities

Mycedium elephantotus is distinguished from other eastern Australian explanate Pectiniidae by the absence of pits of alveoli at the insertion of costae. With few exceptions it is also distinguished by the inclination of the corallites towards the corallum periphery. However, some *Echinophyllia* do show some inclination of the corallites, although all in the present collection have the proximal wall of almost all corallites protruding above the basal plate. This study suggests that *Mycedium* is close to *Physophyllia* Duncan, 1884, especially *P. ayleni* Wells, 1935, the holotype of which is similar to the central parts of large *M. elephantotus* colonies of the present series. Differences between these species are mostly in the degree to which central and peripheral calices protrude and clearly *Mycedium* can have non-protuberant central calices like those of *Physophyllia*, and *Physophyllia* can have protuberant, inclined peripheral calices like those of *Mycedium*.

Figs. 561-563 *Oxypora glabra*.

Figs. 561, 562 From Bullumbooroo Bay, Great Palm Island, same corallum as Fig. 559 (× 5.0).
Fig. 563 From Lizard Island, same corallum as Fig. 560 (× 2.5).

Fig. 561 ▲

Fig. 562 ▼

Fig. 563 ▼

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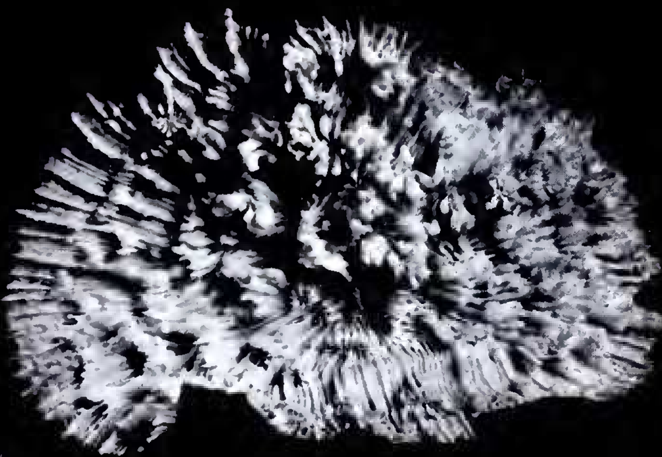

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Distribution

Mycedium elephantotus is common and widely distributed throughout the tropical Indo-Pacific from the Red Sea to Tahiti.

GENUS *PECTINIA* OKEN, 1815

Generic Synonymy

Pectinia Oken, 1815; Faustino (1927); Vaughan & Wells (1943).

Tridacophyllia de Blainville, 1830; Edwards & Haime (1857); Thiel (1932).

Type species *Madrepora lactuca* Pallas, 1766.

Some previous authors have selected *Meandrina pectinata* Lamarck from the West Indies as type species of *Pectinia.* This confusing situation, which is now resolved, is discussed by Chevalier (1975) p. 390.

Introduction and taxonomic history

The most appropriate of the many introductions to this genus was given by Scheer & Pillai (1974). They concluded that the synonymy of nominal species (p. 60) 'is in a hopeless state . . . a critical reading of the available literature on the genus *Pectinia* with careful comparison of the various figures of species will show how difficult it is to pin down the different species'.

Confusion within *Pectinia* has two main origins: firstly the range of variation within species has not been clearly understood and secondly there has been general disagreement about which names are applicable to which (supposed) species.

The 12 nominal species of *Pectinia* are as follows: *Madrepora lactuca* Pallas, 1766; *Tridacophyllia paeonia* Dana, 1846; *Tridacophyllia manicina* Dana, 1846; *Tridacophyllia laciniata* Edwards & Haime, 1849a; *Tridacophyllia symphylloides* Edwards & Haime, 1849a; *Tridacophyllia alcicornis* Saville-Kent, 1871; *Tridacophyllia echinata* Saville-Kent, 1871; *Tridacophyllia cervicornis* Moseley, 1881; *Tridacophyllia rectifolia* Saville-Kent, 1891; *Tridacophyllia elongata* Rehberg, 1892; *Tridacophyllia primordialis* Gardiner, 1899a, *Pectinia plicata* Nemenzo, 1959. Of these, the name *lactuca* has been used by most authors and *paeonia, manicina, laciniata, symphylloides* and *alcicornis* variously used to indicate other supposed species. However, even with *P. lactuca,* descriptions, synonymies and photographs

Figs. 564-568 *Mycedium elephantotus,* Figs. 565-568 (× 0.5).

Fig. 564 From Curacao Island, Palm Islands, collecting station 56 (×0.25).
Fig. 565 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.
Fig. 566 From Hook Island, Whitsunday Islands, collecting station 39.
Fig. 567 From Orpheus Island, Palm Islands, collecting station 55.
Fig. 568 From Yorke Island, collecting station 13.

Figs. 569-580 *Mycedium elephantotus* (× 2.5).

Fig. 569 From Bushy Island-Redbill Reef, collecting station 80.
Fig. 570 From Dido Rock, Palm Islands, collecting station 58.
Fig. 571 From Tijou reef, collecting station 2.
Fig. 572 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.
Fig. 573 From Yorke Island, collecting station 13.
Fig. 574 From the Pompey Reefs, collecting station 75.
Fig. 575 From Bullumbooroo Bay, Great Palm Island.
Fig. 576 From Iris Point, Orpheus Island, Palm Islands, collecting station 55.
Fig. 577 From Hook Island, Whitsunday Islands, collecting station 39.
Fig. 578 From the Swain Reefs, collecting station 76.
Figs. 579, 580 Same corallum from Curacao Island, Palm Islands, collecting station 56.

Fig. 569 ▲

Fig. 570 ▲

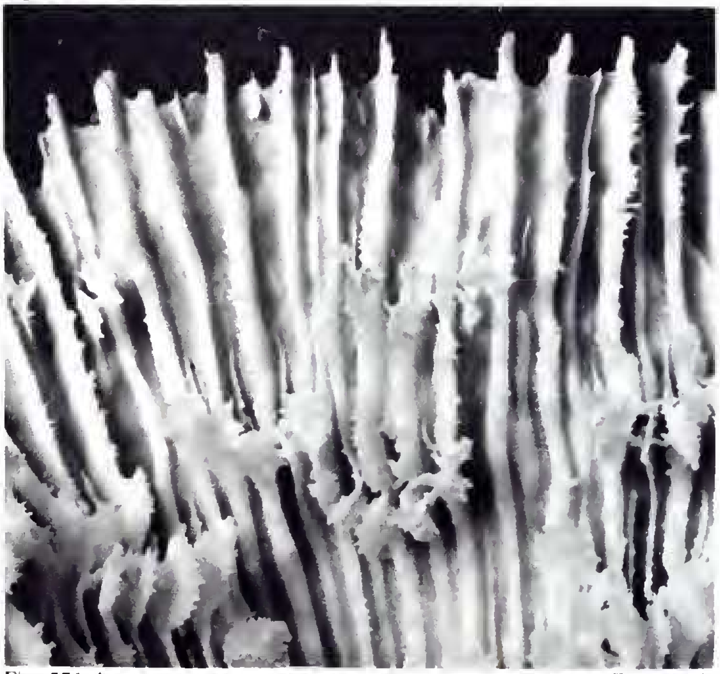

Fig. 571 ▲

Fig. 574 ▲

Fig. 573 ▼

Fig. 572 ▼

Fig. 575 ▲

Fig. 576 ▲

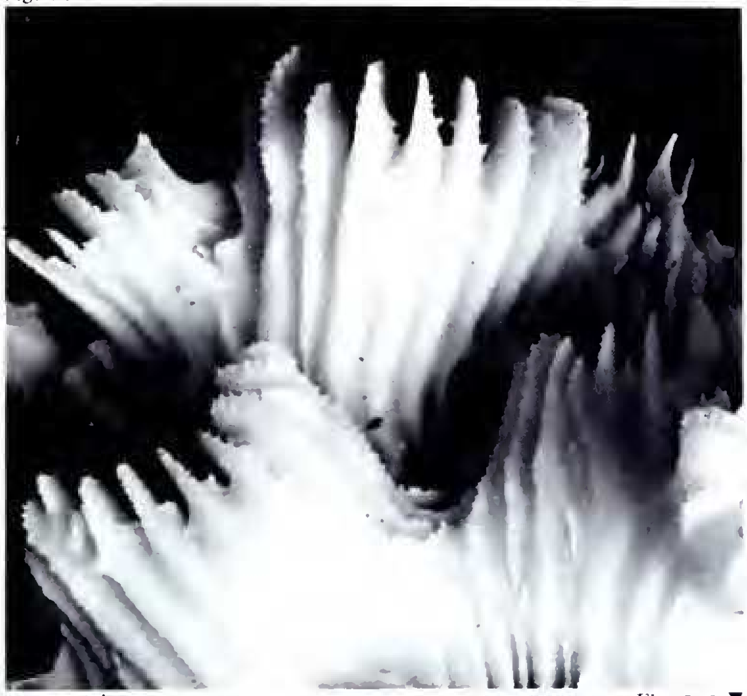

Fig. 577 ▲

Fig. 580 ▲

Fig. 579 ▼

Fig. 578 ▼

are frequently conflicting, and no recent authors have been confident in their distinction between this and other species.

Priority of the genus *Pectinia* Oken (not *Pectinia* of Edwards & Haime) over *Tridacophyllia* was established by Vaughan (1901) although most subsequent authors (including Matthai, 1928; Thiel, 1932; Yabe *et al.* 1936; Umbgrove, 1939) until Crossland (1952) retained the name *Tridacophyllia. Pectinia* was used for the first annotated account of the genus by Faustino (1927), who divided it into 4 species, *P. lactuca, P. paeonia, P. laciniata* and *P. symphylloides* and gave original descriptions of these with translations, illustrations and remarks, but attempted no original discussion or synonymy.

Matthai (1924) used both *Pectinia* and *Tridacophyllia*, the former referred to a West Indian species (see above), the latter referred to *T. lactuca* (Pallas) from the Indo-Pacific. Of the latter, Matthai commented that all four nominal species of Edwards & Haime (*lactuca, laciniata, manicina* and *symphylloides*) may be the same species.

The first comprehensive account of the genus is that of Thiel (1932) who recognised three species, *Tridacophyllia lactuca* (Ellis & Solander, not Pallas), *T. laciniata* and *T. alcicornis* and gave detailed synonymies for the first two. *Tridacophyllia paeonia* is included in the synonymy of *T. laciniata*, establishing these names as supposed alternatives. The other three species names used by Edwards & Haime are combined with others as *T. lactuca. Tridacophyllia elongata* is included in *T. alcicornis.* Thiel explained the confusion caused by juvenile type specimens. He summarised his opinions on the synonymy of *Pectinia* species as follows:

Fig. 581 *Mycedium elephantotus* from the Palm Islands with tentacles retracted during the day.

'*Tridacophyllia primordalis* = ?? *Tridacophyllia lactuca* juv. jev.
Tridacophyllia manicina = *Tridacophyllia lactuca*
Tridacophyllia rectifolia = *Tridacophyllia lactuca*
Tridacophyllia symphylloides = *Tridacophyllia lactuca*
Tridacophyllia cervicornis = ?? *Tridacophyllia laciniata* juv.
Tridacophyllia paeonia = *Tridacophyllia laciniata*
Tridacophyllia elongata = *Tridacophyllia alcicornis*
Tridacophyllia echinata = keine *Tridacophyllia*'

The same three species emerge from the detailed revision of Chevalier (1975) under the names *P. lactuca, P. paeonia* and *P. alcicornis,* although doubts were again expressed about the distinction between them, especially *P. alcicornis.* The latter two species, however, were represented in Chevalier's collection by single specimens only.

The results of the present study conflict greatly with those of previous authors. As with several other scleractinian genera, several detailed regional studies will have to be made before the taxonomy of the genus can be stabilised. For this reason, and because species are hard to identify from photographs, the present account does not include detailed synonymies. However, it is probable that all nominal 'species' except *P. elongata, P. cervicornis* and *P. primordialis* occur within the Great Barrier Reef and that the three species described below incorporate most of the variation of the genus. Clearly, two of these species correspond to the new species described by Dana, *P. paeonia* and *P. manicina,* and that the latter is a junior synonym of *P. lactuca* Pallas,

Fig. 582 *Mycedium elephantotus* from the Swain Reefs with tentacles extended at night.

the type of which is lost. It seems also clear that *P. laciniata* (Edward & Haime) is a junior synonym of *P. paeonia* and that the other three species of Edwards & Haime (noted above) are junior synonyms of *P. lactuca*.

It may be noted here that *P. elongata*, *P. cervicornis* and *P. primordialis* differ very greatly from the other species originally included in *Tridacophyllia* by Thiel. Wells (1954) erected a new genus, *Dactylotrochus*, for *cervicornis* and *primordialis* and placed these two species in synonymy: '*Tridacophyllia cervicornis* Moseley and *T. primordialis* Gardiner slightly resemble *Tridacophyllia* (= *Pectinia*) but none of the specimens show traces of secondary calicular centres or colonial habit.' He included *Dactylotrochus* in the Family Caryophylliidae and pointed out similarities to the genus *Desmophyllum*. *Pectinia elongata* has a superficial resemblance to *D. cervicornis* but clearly belongs to the Pectiniidae if not to *Pectinia*.

Tridacophyllia echinata Saville-Kent, as pointed out by Chevalier (1975), is a valid species of *Echinophyllia* (see p. 307).

Pectinia lactuca (Pallas, 1766)

Synonymy

Madrepora lactuca Pallas, 1766.

Tridacophyllia manicina Dana, 1846; Edwards & Haime (1849a, 1857).

Tridacophyllia lactuca (Pallas); Edwards & Haime (1849a, 1857).

Tridacophyllia symphylloides Edwards & Haime (1849a, 1857).

Tridacophyllia rectifolia Saville-Kent, 1891.

The further synonymies of this species, as proposed by Thiel (1932a) and Chevalier (1975), both differ greatly from the range of growth forms as determined by the present study. The species, as described below, has been illustrated in previous literature as follows: Matthai (1924) Pl. VIII, Fig. 6, ? Pl. III, Figs. 8, 9 (as *lactuca*); Faustino (1927) not Pl. 41 (*lactuca*), Pl. 42, Fig. 2 (as *laciniata*), Pl. 43 (as *symphylloides*); Thiel (1932) not Pl. XVIII, Fig. 3 (*lactuca*), Pl. XXI, Fig. 2 (as *laciniata*); Yabe, Sugiyama and Eguchi (1936) Pl. XXXIV, Fig. 6 (as *alcicornis*), ? Fig. 7 (as *lactuca*), Pl. XXXV, Fig. 3 (as *lactuca*), Fig. 5 (as cf. *alcicornis*); Wells (1856) Fig. 321, 3 (as *lactuca*); Ma (1959) ? Pl. CCLII, Fig. 1 (as *lactuca*); Chevalier (1975) Pl. XXXVI, Fig. 4 (as *lactuca*).

Material studied

Wai Weer Island, Jewell Reef, Palm Islands (6 specimens), **Whitsunday Islands** (4 specimens).

These localities include collecting stations 34, 35, 39, 45, 55, 60, 94, 97, 102, 135.

Previous records from Eastern Australia

Not previously recorded except by a doubtful reference from Crossland (1952).

Characters

Coralla form large horizontal plates, sometimes by overgrowths, with very large radiating valleys up to 4 cm across (Figs. 814-816). Initial budding is circumoral and there is no central corallite. Centres form a single series along the valley axis or occur near the valley floor, not on the collines. They are linked by valley septa. The collines are usually thin and high, usually vertical. Near the base the collines may be thickened by vesicular, endothecal dissepiments. Their upper margins are always thin and have a ragged appearance; usually they are highly perforate. Septo-costae are spaced 2-4 mm apart and are usually 3 mm wide. Most extend from the top of the

collines to the valley floors. They are not arranged in orders but vary continually in size, the longest being thicker and broader than the others. All septo-costae have granulated sides and most have dentate margins, the dentations being very irregularly spaced. Some septa have very low, elongate paliform lobes which may form a low, poorly defined crown. The columellae usually consist of the twisted inner margins of major septa with a few elongate dentations, rotated in a clockwise direction. They may be trabecular but are never well developed. The undersurface of most coralla have long, narrow costae and are irregularly granulated.

Living colonies are mostly uniform in colour, usually grey, brown or green. The coenosarc forms only a very thin layer and tentacles are not commonly expanded even at night. When they are expanded they are long (several cm) and very thin.

Skeletal variation

As with *P. paeonia*, this species is never found in biotopes exposed to strong or moderate wave action. Coralla from the most exposed of the biotopes where it does occur have relatively thick collines and relatively thick septo-costae which have well developed dentations sometimes forming paliform lobes. Columellae are relatively well developed.

Coralla from deep or turbid water have extremely thin collines which are usually highly perforated. Likewise, septo-costae are fine and little ornamented. Columellae seldom consist of more than the twisted inner margins of the major septa.

Affinities

Distinctions between *P. lactuca* and *P. paeonia* are given below (p. 333).

Distribution

Clearly verified records are from Madagascar and the Andaman and Nicobar Islands in the west to the Marshall Islands, New Hebrides and Fiji in the east.

Pectinia paeonia (Dana, 1846)

Synonymy

Tridacophyllia paeonia Dana, 1846.

Tridacophyllia laciniata Edwards & Haime, 1849a; Edwards & Haime (1857).

As with the previous species, the further synonymies proposed by both Thiel (1932) and Chevalier (1975) differ greatly from the range of growth forms as determined by the present study. This species, as described below, has been illustrated in previous literature as follows: Faustino (1927) ? Pl. 41 (as *lactuca*), Pl. 42, Fig. 1 (as *paeonia*); Thiel (1932) ? Pl. XIII, Figs. 1 & 2 (as *laciniata*), Pl. XVIII, Fig. 3 (as *lactuca*); Yabe, Sugiyama & Eguchi (1936) Pl. XXXV, Figs. 1, 2 (as *lactuca* var. *japonica*); Ma (1959) Pl. CCXLIX, CCLI, ? CCLIII, Fig. 1 (as *lactuca*), CCLII, Fig. 2 (as *laciniata*); Scheer & Pillai (1974) Pl. 28, Figs. 1, 2 (as *lactuca*); Chevalier (1975) Pl. XXXVI, Fig. 2 (as *paeonia*).

Material studied

Darnley Reef, Murray Islands, Lizard Island (2 specimens), **Eyrie Reef, Bewick Island, Hope Island, Low Isles** (2 specimens), **Yankee Reef, Palm Islands** (43 specimens), **Whitsunday Islands** (19 specimens), **Pompey Complex** (2 specimens), **Swain Reefs** (4 specimens), **Frigate Cay.**

These localities include collecting stations 12, 13, 18, 19, 30, 32, 34, 36, 37, 39, 41, 42, 43, 45, 52, 55, 57, 58, 59, 60, 68, 69, 72, 81, 91, 97, 98, 102.

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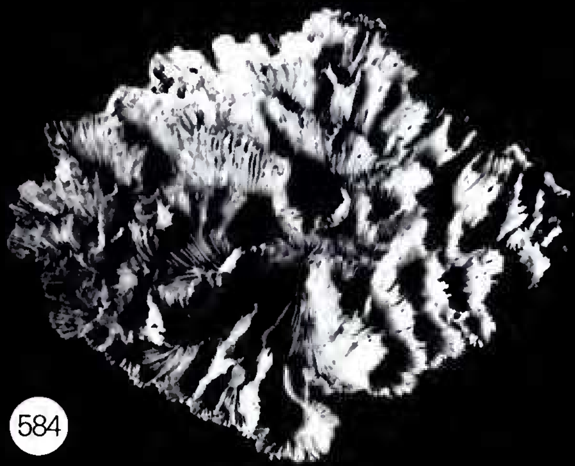

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Previous records from Eastern Australia

Eagle Island (as *Tridacophyllia paenoia*) Crossland (1952); **Low Isles** (as *Tridacophyllia lactuca*) Yonge *et al.* (1932), Yonge (1940).

Characters

Like *P. lactuca*, colonies of *P. paeonia* frequently exceed 1 m diameter (Fig. 817). They have a wide range of growth forms, but unlike *P. alcicornis*, there is relatively little difference between the skeletal characters of juveniles and those of large coralla. Coralla never form extended valleys; centres may be arranged in short series but are usually isolated except for peripheral buds. These are usually deeply seated among the collines with budding usually occurring on the valley floor rather than on the collines. The exotheca may be flattened or cup-shaped, as described for *P. alcicornis* and, like *P. alcicornis*, vertical collines between centres may be plate- or pinnacle-like, the latter formed from the thickening and upward growth of major septo-costae. Septa are not arranged in orders. They vary greatly in size and development, those reaching the columellae having fine, elongate, twisted dentations along their inner margins which comprise much or all of the columella structure. The columellae are always small and trabecular. The rest of the septal margins are smooth or finely dentate. The sides of the septa are smooth or very finely granulated.

Living colonies (Figs. 817, 818) have uniform dull colours, usually blue-grey or grey-brown.

Skeletal variation

As with other *Pectinia* species, *P. paeonia* only occurs in relatively protected biotopes. Coralla from the most exposed of these biotopes have pinnacle-like collines with well developed exo- and endothecae. Septa are usually finely dentate and columellae clearly developed. Those from very protected biotopes are extremely delicate. Septa are very fine and smooth and irregular in appearance. Collines are very thin, twisted and irregular and are entirely exothecal. The columellae become increasingly reduced and eventually absent.

Affinities

Pectinia lactuca is readily distinguished from *P. paeonia* by having radiating valleys. It is almost always possible to trace a continuous valley from the corallum periphery to its centre. This is never the case in *P. paeonia*, where extratentacular budding occurs irregularly and series of centres are not formed. The collines of *P. lactuca* are continuous and plate-like, not bisected and irregular as in *P. paeonia*, where only the upcurved margins of exotheca surrounding one or a few centres form vertical plates.

Pectinia paeonia from relatively exposed biotopes is less easily distinguished from *P. alcicornis*. Differences between these species are discussed on p. 338.

Distribution

Uncertainties in the identification of *P. paeonia* (as well as other *Pectinia* species) make its geographic distribution difficult to determine. The species has clearly been recorded from Ceylon, the Nicobar Islands, Indonesia, the Philippines, the China Sea, New Caledonia, the Great Barrier Reef and Fiji.

Figs. 583-585 *Pectinia lactuca* (× 0.33).

Figs. 583, 585 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.
Fig. 584 From the Palm Islands.

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Pectinia alcicornis (Saville-Kent, 1871)

Synonymy

Tridacophyllia alcicornis Saville-Kent, 1871; Yabe, Sugiyama & Eguchi (1936).

Pectinia alcicornis (Saville-Kent); Chevalier (1975).

All three publications give clear illustrations of this species.

Material studied

Big Mary Reef, Yorke Island (3 specimens), **Murray Islands** (3 specimens), **Lizard Island** (2 specimens), **Hope Island, Low Isles, Bowl Reef, Palm Islands** (49 specimens), **Gould Reef, Whitsunday Islands** (42 specimens), **Swain Reefs** (2 specimens).

These localities include collecting stations 10, 11, 12, 13, 27, 28, 29, 34, 35, 39, 41, 42, 43, 45, 55, 57, 58, 59.

Previous records from Eastern Australia

Not previously recorded.

Characters and growth form variation

Variation in the skeletal characters of *P. alcicornis* is so great that very few are common to all the coralla of the present series. This variation is firstly a result of a progression of growth stages in small coralla, and secondly is environmentally induced.

Initial growth stages are illustrated in Figs. 596-600. Monocentric coralla may attain a maximum diameter of 15 cm and usually have well defined calicular characters. Septo-costae vary greatly in length, thickness and ornamentation. The major septo-costae (which are seldom clearly arranged in orders) are thicker than the others and usually have a series of lobed dentations with a large inner paliform lobe. Some of these increase greatly in height and thickness as they radiate from the calice centre and eventually take the form of a wall. Adjacent septa curve to grow up these walls which subsequently develop into collines. Daughter corallites bud in irregular positions on the newly formed collines or at their bases.

In subsequent development both the growth form and the calicular characters of colonies vary greatly according to prevailing environmental conditions. Coralla from biotopes exposed to currents or some wave action in partly turbid biotopes (especially associated with high islands) are relatively densely calcified and consist of very irregular sub-digitate tapering branches (Fig. 604) or flat plates from which branches arise (Fig. 603).

Calices of such colonies are relatively small (1-2 cm diameter) and indistinct. Columellae are weakly developed and usually consist of a few trabeculae only. Septa are thick, regularly spaced and seldom anastomosed. Costae are usually thick and smooth and have very reduced ornamentation. Both endotheca and exotheca are well developed.

Figs. 586-593 *Pectinia paeonia* (× 0.5).

Fig. 586	From Low Isles.
Figs. 587, 588	From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.
Fig. 589	From Happy Bay, Long Island, Whitsunday Islands, collecting station 102.
Figs. 590-593	From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97, showing growth form variation in a single biotope.

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Fig. 594 ▲

Figs. 594, 595 *Pectinia paeonia.*

Fig. 594 From the Pompey Complex, collecting station 72 (× 0.8).
Fig. 595 From Pioneer Bay, Orpheus Island, Palm Islands, collecting station 91 (× 1.5).

Coralla exposed to currents or some wave action in clear reef water tend to be less sub-digitate but have a more bushy appearance, with collines never forming flat or regular plates. Rather, they are greatly contorted and regularly bisected, so that an individual colline is composed of only a very few septa. These have irregular dentations including very fine branching dentations at the colline margins which subsequently form new divisions in the collines. All septa and dentations are granulated, the latter frequently forming transverse rows across the costae. Budding usually occurs well below the upper margins of the collines. Calices are deep and well defined with large trabecular or spongy columellae. Septo-costae have a highly irregular appearance, frequently branching and anastomosing.

At the limit of their growth range, individual corallites are cup-shaped with ragged but entire margins.

Underwater, *P. alcicornis* is also distinguished by its colour. In contrast to the greys and dull browns of the other species, *P. alcicornis* colonies are usually mixtures of pink, yellow, green and brown, usually with the colony extremities being paler and a different colour from the central parts (Fig. 821).

Fig. 595 ▲

Affinities

This species is distinguished from *P. paeonia* by its strong septal dentations (which are conspicuous even underwater) and relatively large columellae. It is also usually distinguished by its growth form (as illustrated) although there is so much range in *P. alcicornis* that growth forms can be similar. *Pectinia alcicornis* is usually more heavily calcified than *P. paeonia* with generally thicker and coarser skeletal structures.

Pectinia elongata, previously considered synonymous with *P. alcicornis* (Thiel, 1932; Chevalier, 1975) is illustrated in Fig. 605. This species has a completely different growth form in being entirely branching with thin tapering branches. It has not been found on the Great Barrier Reef, although its presence could be predicted on biogeographic grounds.

Distribution

Confirmed records are from Indonesia, New Caledonia, Palao, the Solomon Islands, the Great Barrier Reef and Addu Atoll.

Figs. 596-600 Early growth stages of *Pectinia alcicornis*, Figs. 596-599 (× 0.7).

Figs. 596, 600 From Fantome Island, Palm Islands, collecting station 34; Fig. 600(× 0·3).
Figs. 597, 599 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.
Fig. 598 From Pioneer Bay, Orpheus Island, Palm Islands, collecting station 91.

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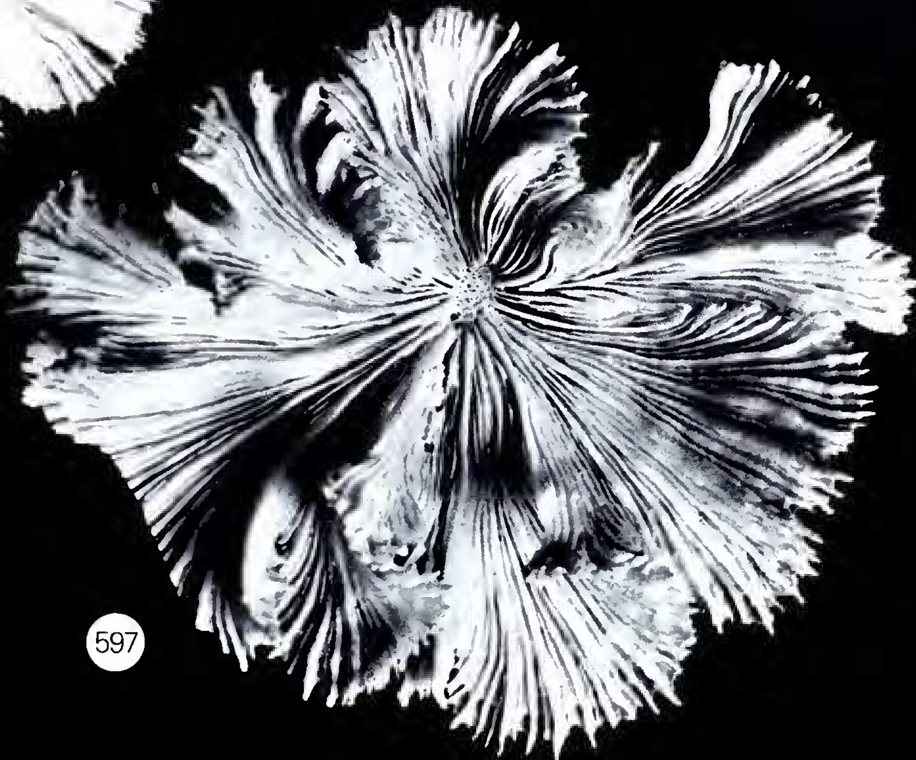

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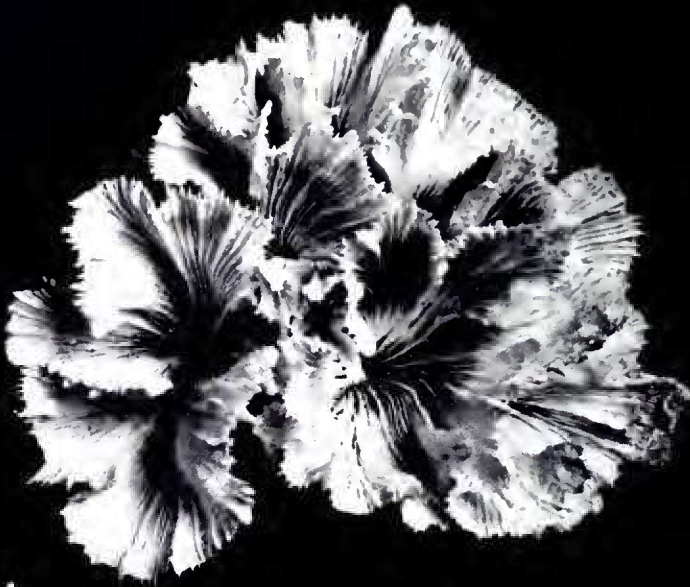

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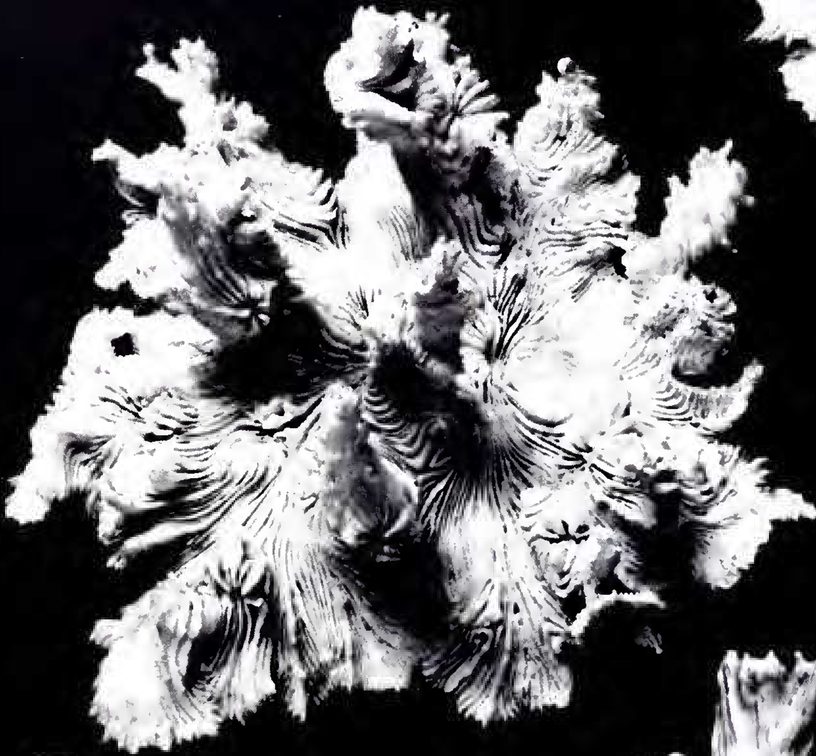

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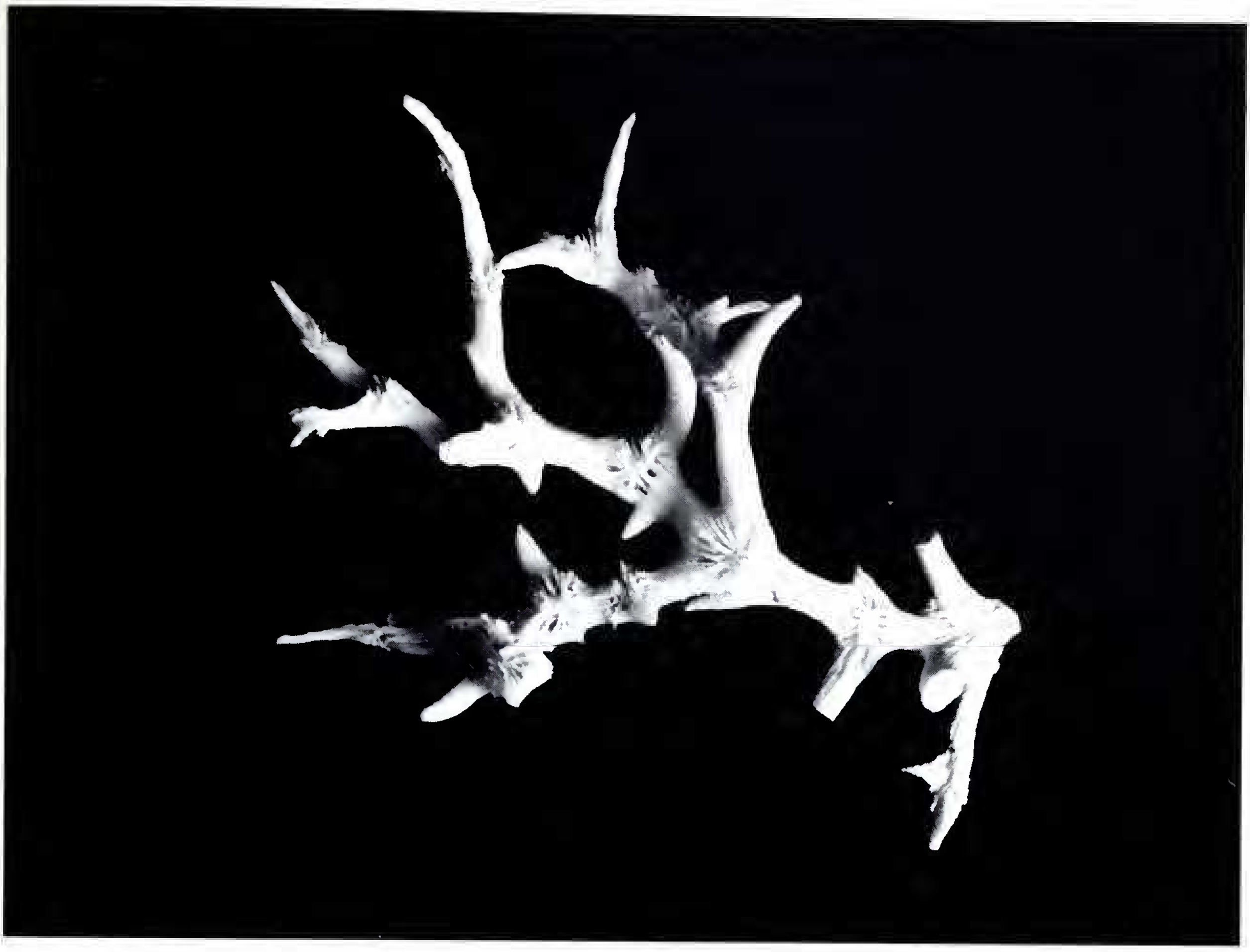

Fig. 605 *Pectinia elongata* from Conflict Atoll, Louisiade Archipelago (× 1.2).

Figs. 601-604 *Pectinia alcicornis* (× 0.5).

Fig. 601 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.
Fig. 602 From Hook Island, Whitsunday Islands, collecting station 39.
Fig. 603 From Butterfly Bay, Hook Island, Whitsunday Islands, collecting station 98.
Fig. 604 From Bullumbooroo Bay, Great Palm Island, collecting station 35.

X
Family Caryophylliidae Gray, 1847

This large family is divided by Vaughan & Wells (1943) into six subfamilies, only one of which, subfamily Eusmiliinae Edwards & Haime, 1857, is hermatypic. The large number of ahermatypic species have a world-wide distribution and are abundant along eastern Australia in deep water. They are also frequently found in shallow reef waters with hermatypic species.

SUBFAMILY EUSMILIINAE EDWARDS & HAIME, 1857

All species are hermatypic and colonial. All have large, exsert, widely separated septa which have little or no ornamentation. Costae are reduced, columellae reduced or absent. Corallite walls are septothecal or parathecal. The endotheca is vesicular. Polyps are large and have major specific differences in structure.

GENUS *EUPHYLLIA* DANA, 1846

Generic synonymy

Euphyllia Dana, 1846; Matthai (1928); Vaughan & Wells (1943).

Type species *Caryophyllia glabrescens* Chamisso & Eysenhardt, 1821.

Characters

Colonies are phaceloflabellate with corallites in long or short laterally free series. Corallite walls are septothecal. Columellae are absent or very reduced. Polyps are large with elongate tentacles expanded day and night. Morphological differences between species are seen primarily in the polyps rather than in the skeletons.

SUBGENUS *EUPHYLLIA* NEW SUBGENUS

Euphyllia is the nominate subgenus established for *Euphyllia* species not included in subgenus *Fimbriaphyllia.* Most nominal species of *Euphyllia* are junior synonyms of either *E.* (*Fimbriaphyllia*) or *E.* (*Euphyllia*) *glabrescens,* hence the present subgenus includes a small number of species, perhaps only the two described below. These have, in common, a similar polyp structure (Figs. 822, 823) and a similar phaceloid growth form.

Euphyllia (Euphyllia) glabrescens (Chamisso & Eysenhardt, 1821)

Synonymy (partly after Matthai, 1928)

Caryophyllia glabrescens Chamisso & Eysenhardt, 1821; Ehrenberg (1834).

Caryophyllia angulosa Quoy & Gaimard, 1824.

Lobophyllia glabrescens (Chamisso & Eysenhardt); de Blainville (1830, 1834).

Euphyllia glabrescens (Chamisso & Eysenhardt); Dana (1846); Edwards & Haime (1851c, 1857); Tenison-Woods (1878); Quelch (1886); Bourne (1888); Gardiner

(1899a, 1904); Vaughan (1918); Hoffmeister (1925); Matthai (1924, 1926, 1928); Faustino (1927); Yabe, Sugiyama & Eguchi (1936); Crossland (1952); Wells (1954); Searle (1956); Ma (1959); Nemenzo (1960); Chevalier (1971); Scheer & Pillai (1974).

Euphyllia turgida Dana, 1846; Edwards & Haime (1851c, 1857); Studer (1881); Quelch (1886); Gardiner (1904); Matthai (1924, 1926, 1928); Thiel (1932); Ma (1959).

Euphyllia rugosa Dana, 1848; Edwards & Haime (1851c, 1857); Duncan (1884); Quelch (1886); Bedot (1907); Ma (1959).

Leptosmilia glabrescens (Chamisso & Eysenhardt); Edwards & Haime (1848b).

Leptosmilia rugosa (Dana); Edwards & Haime, 1848b.

Leptosmilia costulata Edwards & Haime, 1848b.

Leptosmilia gaimardi Edwards & Haime, 1848b.

Leptosmilia striata Edwards & Haime, 1848b.

Euphyllia costulata (Edwards & Haime); Edwards & Haime (1851c, 1857).

? *Euphyllia gaimardi* (Edwards & Haime); Edwards & Haime (1851c, 1857); Ortmann (1889).

Euphyllia striata (Edwards & Haime); Quelch (1886); Ortmann (1889).

Euphyllia laxa Gravier 1910; Gravier (1911).

Edwards & Haime (1848b) included five of the above nominal species of *E. glabrescens* in their *Leptosmilia* viz: *L. glabrescens*, *L. costulata*, *L. striata*, *L. rugosa*, and *L. gaimardi*, the latter a re-naming of *Caryophyllia angulosa* Quoy & Gaimard. In 1851 the genus *Euphyllia* was adopted by Edwards & Haime and eight extant species were referred to it. Of these, Vaughan (1918) synonymised *E. rugosa* and *E. gaimardi* with *E. glabrescens* and Matthai (1928) added *E. costulata* and *E. striata*. Crossland (1952) also placed *E. laxa* in *E. glabrescens*, an opinion supported by Chevalier (1971), who gives a good account of the synonymy of the species.

Material studied

Darnley Island (3 specimens), **Dungeness Island** (11 specimens), **Murray Islands** (3 specimens), **Jervis Reef, Northwest Reef** (3 specimens), **Thursday Island** (4 specimens), **Palm Islands** (8 specimens), **Pandora Reef, Whitsunday Islands** (15 specimens), **Bushy Island-Redbill Reef** (3 specimens), **Swain Reefs** (2 specimens), **Heron Island.**

These localities include collecting stations 13, 14, 27, 29, 35, 38, 39, 54, 68, 80, 95, 96, 97, 101, 102, 111, 116, 119, 122, 140.

Previous records from Eastern Australia

Torres Strait, Quelch (1886); **Murray Islands**, Vaughan (1918), Mayer (1918); **Low Isles**, Yonge & Nicholls (1931); **Batt Reef**, Yonge (1940), Crossland (1952).

Characters

The growth form of this species varies greatly from a purely phaceloid condition to one where some parts may be phaceloflabellate. Within individual coralla, the frequency of branching, the diameter of branches and the distance between branches are relatively uniform but these characters vary greatly among coralla of differing

Figs. 606-608 *Euphyllia glabrescens* (× 0.7).

Fig. 606 From Darnley Island, collecting station 31.
Fig. 607 From North-West Reef, collecting station 14.
Fig. 608 From Thursday Island, collecting station 54.


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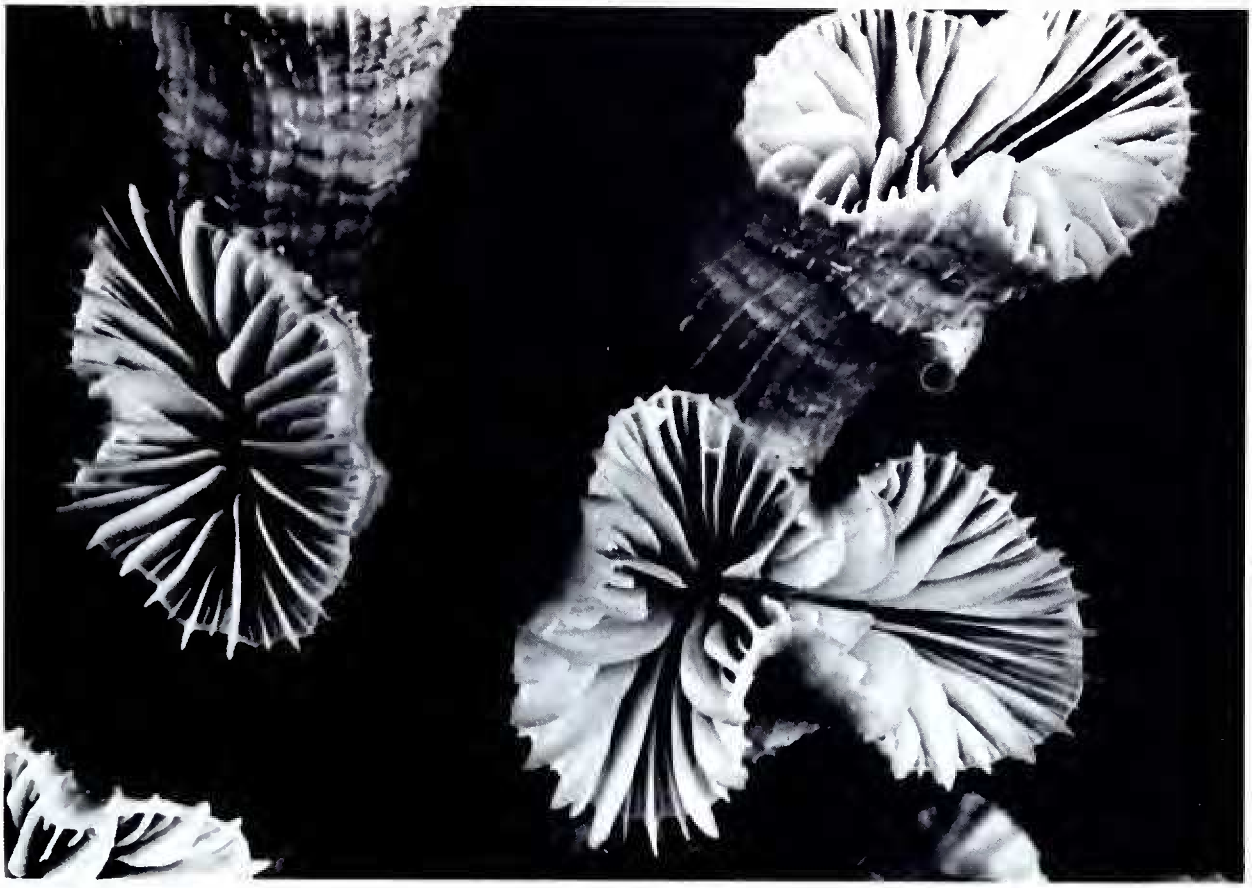

Fig. 609 *Euphyllia glabrescens* from Thursday Island, same corallum as Fig. 608 (× 2.4).

Fig. 610 *Euphyllia glabrescens* from Bushy Island-Redbill Reef, showing tentacles extended during the day.

sizes and from different environments. Branch diameters immediately after branching range from 13 to 31 mm; those from large coralla remain relatively uniform in size, those from small ones expand rapidly to maintain a uniform distance between branches. This distance averages approximately 7-16 mm and is not correlated with branch diameters. Large coralla tend to have a high proportion of monocentric branches and branch infrequently; small ones, with a relatively large growing surface, have many centres and consequently a flabellate form.

Usually four orders of septa can be distinguished but a fifth may be present. First and second orders are usually slightly exsert and extend inwards for most of the calice radius before plunging vertically or near vertically. Their inner margins may be twisted or folded towards the centres or thickened around the centres or form a few trabeculae. There are no other columella structures. All septa are finely granulated. The wall is very thin around the upper margin and becomes thickened by exothecal dissepiments which in some coralla (from deeper water) are very prominent. Development of the costae varies greatly; in some coralla they form only fine striations, in others they are prominent, sometimes ornamented by lobes or even spines.

Polyps have a uniform appearance. They are expanded day and night with tentacles forming a continuous cover obscuring the skeletal branches. Tentacles are tubular, grey-blue to grey-green in colour with cream or white tips (Figs. 610, 822, 823). They are normally straight, radiating from the polyps, but sometimes become flaccid. It may be noted that, whereas this species has a relatively uniform colour along eastern Australia, it may have markedly different colours in

Fig. 611 *Euphyllia cristata* from Jewell Reef (× 0.7).
Fig. 612 *Euphyllia cristata* from the Murray Islands (× 1.6).

Fig. 611 ▼

Fig. 612 ▼

Figs. 613, 614 *Euphyllia cristata* from the Murray Islands, the same corallum as Fig. 612 (× 5.0).

other geographic regions, e.g. it is mustard-yellow at Enewetak Atoll, Marshall Islands.

Affinities

Euphyllia glabrescens is common on the Great Barrier Reef and distinctive underwater. It closely resembles *E. cristata* but is distinguished from it by the characters noted in the affinities of that species.

Distribution

Widely distributed throughout the Indo-Pacific from the Red Sea east to the Marshall Islands and Samoa.

Euphyllia (Euphyllia) cristata Chevalier, 1971

Synonymy

Euphyllia cristata Chevalier, 1971.

Material studied

Murray Islands (2 specimens), barrier reef E of **Murray Islands, Thursday Island, Great Detached Reef, Jewell Reef, Yonge Reef, Palm Islands** (6 specimens), **Swain Reefs** (2 specimens), **Heron Island.**

These localities include collecting stations 1, 3, 30, 35, 37, 38, 54, 77, 90, 110, 139.

Previous records from Eastern Australia

Not previously recorded.

Characters

The present series of specimens shows relatively little variation and all clearly belong to this species, previously known only from a single specimen described in detail by Chevalier. Colonies are phaceloid, dome shaped, <12 cm diameter. They have compact branches which maintain a uniform distance from each other with averages varying from 4 to 8 mm in different coralla. Branches have 1-3 centres and branching occurs at frequent intervals by the formation of constrictions which usually become traversed by septa.

Up to five orders of septa may be distinguished although in parts of some coralla the septa become very irregular and orders indistinguishable. First order septa are up to 4 mm exsert, and extend outwards above and beyond the thecae, especially in small coralla where branch diameters increase rapidly relative to linear growth. The margins of first order septa are usually strongly curved with septa extending almost to the calice centres. Septa of higher orders become progressively reduced until those of the fifth order, when present, are fine ridges only. The sides of septa are glabrous or very finely granulated and their margins are usually finely serrated. Centres are indistinct, but as noted by Chevalier, may be recognised by the folding or curving of septa towards them. Costae of at least three orders are present and are mostly well developed, especially those of the first order which may develop lobes or spines which are sometimes prominent. The walls are thin, especially towards their upper margins. Some development of exothecal dissepiments is visible in some coralla while vesicular endothecal dissepiments are well developed lower in the calices.

Figs. 615-618 *Euphyllia (Fimbriaphyllia)* (× 0.4).

Fig. 615 From Great Palm Island.
Fig. 616 From Great Palm Island, collecting station 92.
Fig. 617 From Juno Bay, Fantome Island, Palm Islands, collecting station 43.
Fig. 618 From Sue Island, collecting station 17.

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Fig. 619 ▲

Fig. 620 ▲

Fig. 621 ▼

Fig. 622 ▼

Polyps are expanded day and night. Tentacles are green with pale orange, yellow or cream tips. They are tubular, essentially similar to those of *E. glabrescens.*

Affinities

This little known species is close to *E. glabrescens.* It is primarily distinguished by being more compact, with branches remaining in close proximity to each other. Septa are more exsert, especially those of the first order, although this may be less conspicuous in larger coralla. As noted by Chevalier, there are further minor differences: first order costae form an acute angle with the septa and they are more prominently ornamented; septa are glabrous or nearly so; a fifth order of septa may be present. The last two characters, however, are of very little use.

Chevalier notes that *E. gaimardi* Edwards & Haime, the type of which is lost, may belong to this species. However, as this cannot be established with any certainty, the present authors agree that a new name is justified.

Distribution

This species is previously known only from the holotype from New Caledonia.

SUBGENUS *FIMBRIAPHYLLIA* NEW SUBGENUS

This subgenus includes *E. fimbriata* and its synonyms as determined by skeletal morphology. The two species described below, however, can be distinguished by the structure of their polyps only, and in this respect are unique in scleractinian taxonomy. The specific name *E. fimbriata* has been dropped *nomen dubium* as the structure of the polyps is unrecorded and the type locality unknown.

In his original description of *Catalaphyllia*, Wells (1971a) wrote '*Euphyllia fimbriata* is alone among several species of *Euphyllia* in having a flabello-meandroid growth form, and it may prove, when the polyps are examined, to be a second species of *Catalaphyllia*'. The polyp structure of these two genera, however, remains very distinct, and clearly *Catalaphyllia* has both skeletal and polyp structures which justifiably separate it from *Euphyllia.* A similar situation applies to *Plerogyra* and *Euphyllia* (*Fimbriaphyllia*) which are also clearly distinguished on the basis of polyp structure but may have similar skeletons.

Synonymy of the subgenus

Madrepora fimbriata Spengler, 1799.

Euphyllia meandrina Dana, 1846; Edwards & Haime (1851c).

Rhipidogyra daniana Edwards & Haime, 1848b.

Rhipidogyra plicata Edwards & Haime, 1848b.

Euphyllia plicata (Edwards & Haime); Duncan (1886).

Euphyllia fimbriata (Spengler); Edwards & Haime (1857); Verrill (1864); Studer (1881); Ortmann (1888); Bedot (1907); Vaughan (1918); Matthai (1924, 1928); Yabe, Sugiyama & Eguchi (1936); Crossland (1952); Searle (1956); Ma (1959); Nemenzo (1960); Chevalier (1971); Zou (1975a).

Euphyllia plicata (Edwards & Haime), the former type species of *Catalaphyllia* Wells, is replaced in synonymy with *E. fimbriata* following re-examination of the type specimen.

Figs. 619-622 *Euphyllia (Fimbriaphyllia)* (× 2.5).

Fig. 619 From Sue Island, same corallum as Fig. 614.
Fig. 620 From Great Palm Island, same corallum as Fig. 611.
Fig. 621 Holotype of *Euphyllia (Fimbriaphyllia) divisa* from Whitehaven, Whitsunday Islands, collecting station 95.
Fig. 622 From Jewell Reef.

Previous records from Eastern Australia (as *E. fimbriata*)

Albany Passage, Warrior Reef, Thursday Island, Port Molle, Matthai (1928); **Batt Reef,** Crossland (1952); **Heron Island,** Stephenson & Wells (1955).

Skeletal characters of the subgenus

Coralla are flabelloid to flabello-meandroid depending mainly on size. Small, flabelloid coralla initially develop a crescentic form (as does *Catalaphyllia*) from which irregular branches develop. Larger coralla are dome-shaped with long sinuous to straight valleys which are usually interconnected. The width of the valleys varies greatly, depending on environmental conditions and the corallum size. Large coralla, which are mostly restricted to protected, partly turbid water, usually have narrow valleys. Coralla in early stages of development have wide valleys, usually with fluted margins. They are in the process of relatively rapid lateral growth and hence valleys are wide and thecae often greatly thickened by dissepiments.

The development of the septa is also variable and also depends on environmental conditions and corallum size. Large coralla and those from turbid biotopes have small, relatively regular septa which are only slightly exsert and which are usually in three regular orders with an abortive fourth order. Small coralla and those from more exposed biotopes have more irregular septa. Some may be exsert up to 1 cm, others only fine ridges with orders often difficult to distinguish. All septa are glabrous or finely dentate and frequently have finely serrated margins. The larger septa extend to, or nearly to, the valley axis or calice centre and have vertical or subvertical inner

Fig. 623 *Euphyllia (Fimbriaphyllia) ancora* (left) and the holotype of *Euphyllia (Fimbriaphyllia) divisa* (right) from the Swain Reefs. Colonies were collected from the same biotope and photographed in an aquarium with tentacles extended.

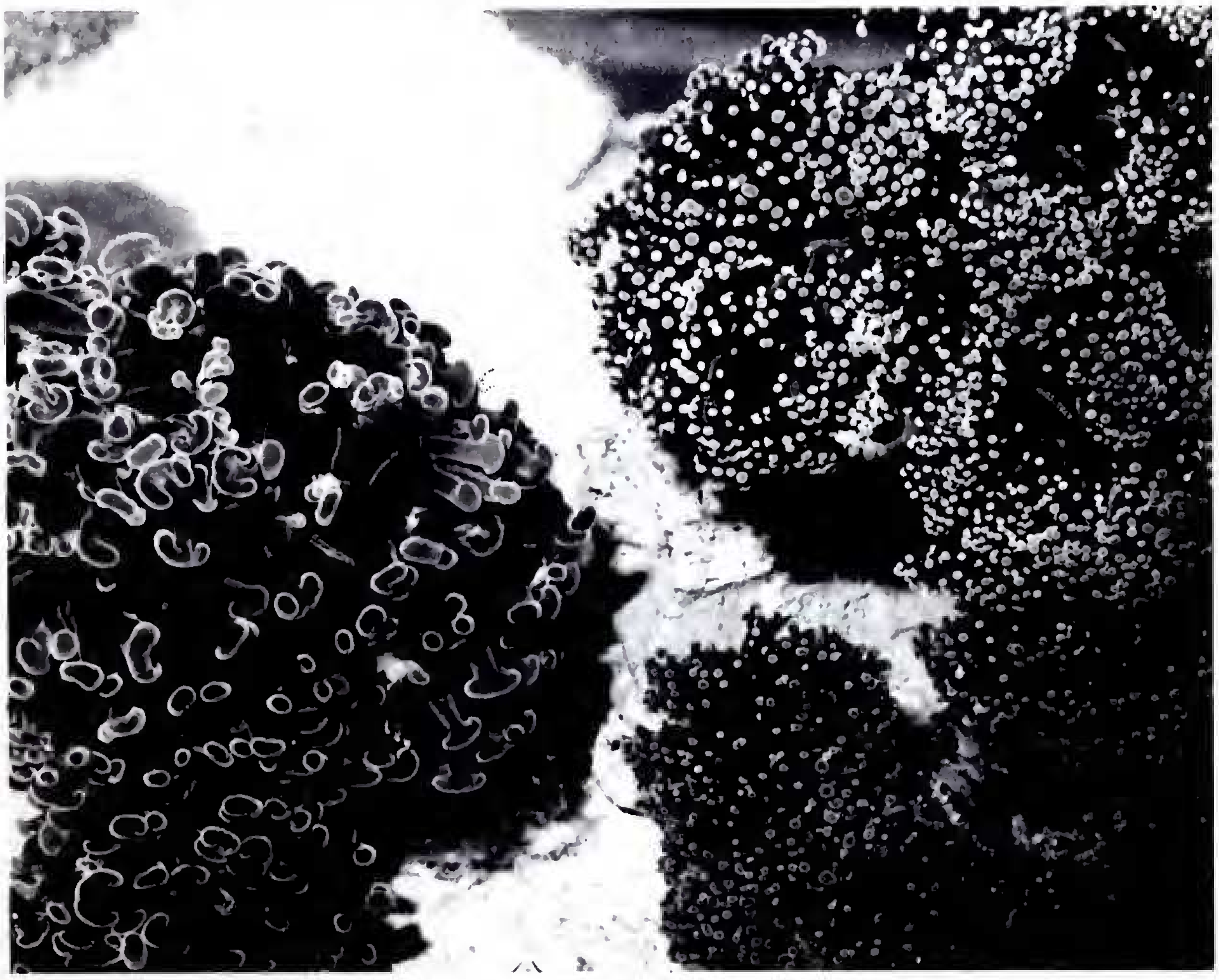


Fig. 624 ▲

Figs. 624, 625 *Euphyllia (Fimbriaphyllia) divisa.*

Fig. 624 From the Swain Reefs, showing a single colony approximately 1.5 m across.
Fig. 625 From the Swain Reefs, showing ramose tentacles expanded during the day.

Fig. 625 ▼

margins which may be folded or curved towards the centres. Some septa have broad inner margins which may become slightly dentate. There are no columellae. The development of the costae varies greatly depending on the degree to which the septa are exsert and the degree of development of the exothecal dissepiments. In some coralla, the costae appear only as fine striations, in others they are lobed or form spines which, as with *E. glabrescens*, may develop into buds. Some coralla show pronounced development of endothecal dissepiments but this is usually restricted to small coralla or those growing in exposed biotopes where lateral growth is pronounced.

Affinities of the subgenus

As noted by Matthai, some coralla may come close to some *Plerogyra sinuosa*. Both may have very exsert, irregular septa and pronounced endothecal depositions. In such cases, *Plerogyra sinuosa* is distinguished by a lack of ordering in the septa and by having more irregular septa. Coralla of this subgenus are also similar to those of *Catalaphyllia jardinei*. The latter is distinguished by having open V-shaped valleys with the major septa almost straight margined and scarcely exsert and there may be some development of columellae. Also, *Catalaphyllia* coralla usually show no sign of having been attached to a substrate.

Within *Euphyllia*, young coralla of the present group may be difficult or impossible to distinguish from the other species, especially *E. glabrescens*, which may have almost identical septa. Larger coralla are readily distinguished by their differing growth forms.

The above account of this subgenus is based entirely on skeletal characters. Species distinctions within the subgenus are made on the characters of the polyps. These differ sufficiently from each other to make species differences clear, yet are sufficiently similar to group them apart from the other subgenus of *Euphyllia* and from the other flabello-meandroid Eusmillidae, *Catalaphyllia* and *Plerogyra*.

Euphyllia (Fimbriaphyllia) *divisa* **n. sp.**

Material studied

Warrior Reef, Murray Islands, Wai Weer Island, Palm Islands, Pandora Reef, Whitsunday Islands (10 specimens), **Pompey Complex, Swain Reefs.**

These localities include collecting stations 28, 39, 59, 71, 77, 97, 98, 111, 121, 135, 140.

Previous records from Eastern Australia

See records of the subgenus. The species has not been previously recognised as distinct from *E.* (*F.*) *ancora.*

Characters

Skeletal characters are as described for the subgenus.

Polyps are extended day and night. They are large and fleshy so that when expanded they obscure the form of the skeleton (Fig. 624). When fully expanded the tentacles may reach a length of 8 cm. They are thick at their base and send off many irregular side branches along their length (Figs. 825, 826). Frequently they divide one or more times; the number of sub-branches may be 20 or more. Each sub-branch has a grey or white cap similar to those of *E. glabrescens*. The rest of the polyps are blue-grey to pale orange.

This species is probably the most common *Euphyllia* of the Great Barrier Reef. It is normally found in partly protected biotopes, usually on horizontal soft sand or rubble substrate.

Skeletal variation

The present series represents the full range of variation described for the subgenus.

Etymology

Named for the appearance of the expanded tentacles.

Holotype (Figs. 621, 623)

Dimensions: Maximum dimension is 16.3 cm. An entire colony.

Locality: Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.

Depth: 5 m.

Collector: J.E.N. Veron.

Holotype: British Museum (Natural History).

Paratypes

Australian Institute of Marine Science.
Queensland Museum, Australia.

Distribution

Known only from the Great Barrier Reef as the present species distinct from the subgenus.

Figs. 626, 627 *Euphyllia (Fimbriaphyllia) ancora* from the Swain Reefs with tentacles extended, showing variation frequently found within the one biotope.

Euphyllia (Fimbriaphyllia) ancora n. sp.

Material studied

Bramble Cay, Darnley Island, Yorke Island (7 specimens), **Murray Islands** (3 specimens), **Sue Island, Wai Weer Island, Thursday Island, Jewell Reef, Palm Islands** (2 specimens), **Whitsunday Islands** (19 specimens).

These localities include collecting stations 13, 17, 26, 28, 30, 39, 54, 59, 97, 98, 125, 126, 128, 135, 140.

Previous records from Eastern Australia

See records of the sub-genus. This species has not been previously recognised as distinct from *E. (F.) divisa*. It is illustrated in Saville-Kent (1893) (Chromoplate IV, I, la-f.) as *Rhipidogyra* sp. (*P. laxa*).

Characters

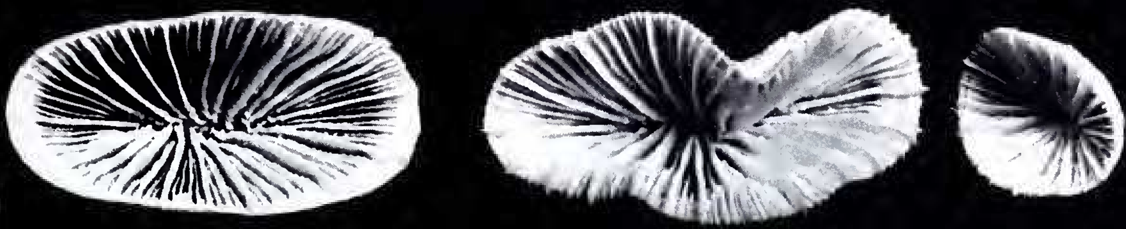
Skeletal characters are as described for the sub-genus.

Polyps are extended day and night. They have very long tentacles which do not branch except at their base. The ends of the tentacles (Figs. 827-829) usually have a pale cap (as have those of other *Euphyllia*) which is curved or crescentic in shape, frequently with the ends of the cap recurved inwards, towards the tentacle stem. In some coralla they may be little more than kidney or anchor shaped (Fig. 626), in others they are sufficiently curved to be scroll-like (Fig. 627). The end of the cylindrical tentacle shaft has a pale band of tissue which is connected on the proximal side to a single ciliated tract which runs down the shaft and on the distal side to a narrow expanding band of tissue which connects the shaft to the tentacle cap. The whole appearance is one of an open-sided funnel with a ciliated inner surface and a ciliated

Fig. 628 Holotype of *Euphyllia (Fimbriaphyllia) ancora* from the Swain Reefs (× 2.5). Fig. 623 shows the living colony.

Figs. 629-634 Growth stages of *Catalaphyllia jardinei.*

Fig. 629	From Juno Bay, Fantome Island, Palm Islands, collecting station 43 (× 1.0).
Fig. 630	From Great Palm Island (× 1.0).
Fig. 631	From Lizard Island (× 1.0).
Fig. 632	From Jervis Reef, collecting station 119 (× 1.0).
Figs. 633, 634	From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97 (× 0.5).



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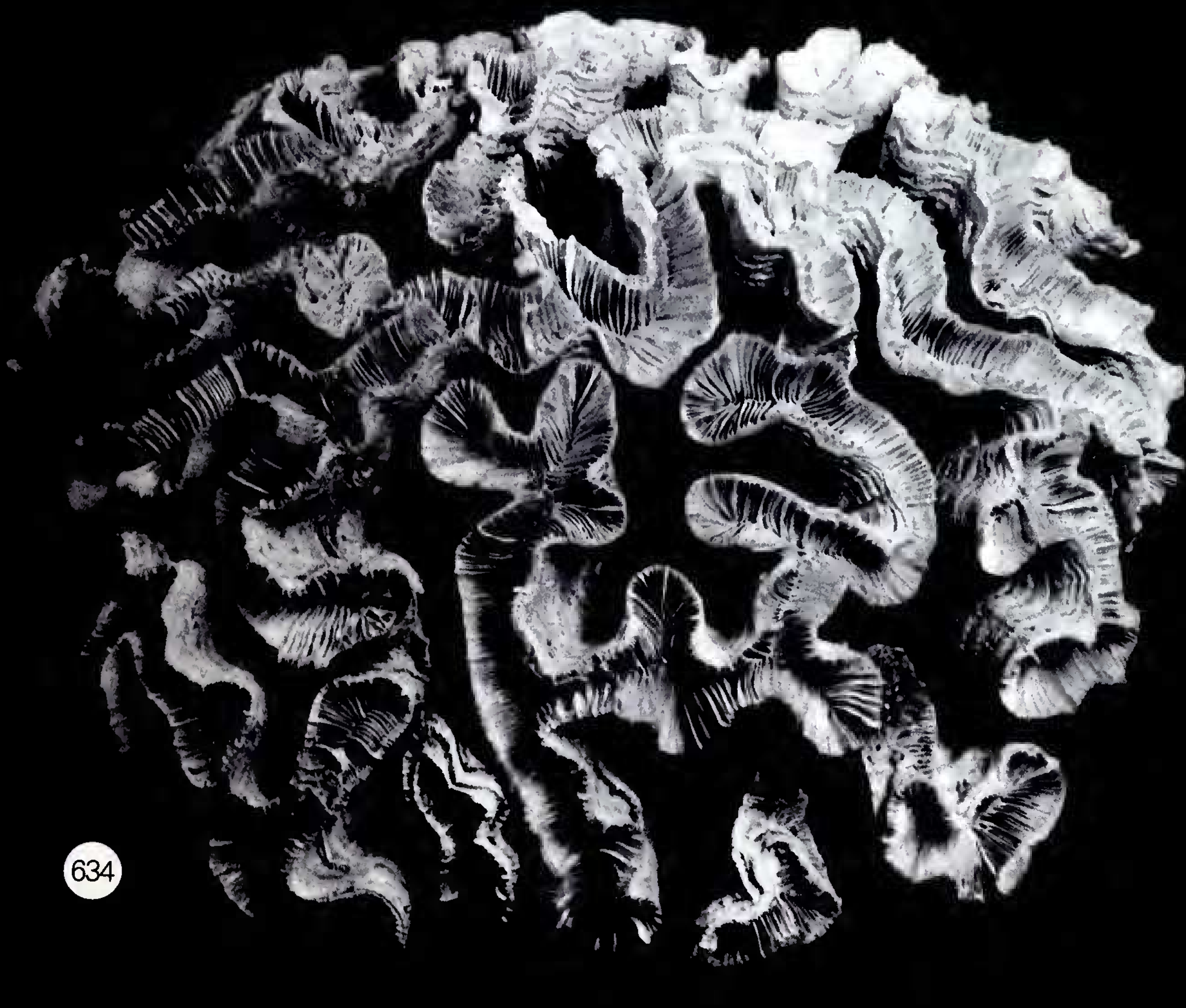

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tract at the bottom leading to the stomodaeum. The tentacle shafts and oral disc are blue-grey to orange in colour.

This species is common on the Great Barrier Reef. It occupies the same biotope as *E. divisa* and both species are frequently found together.

Skeletal variation

The present series has the full range of variation described for the subgenus.

Etymology

Named for the anchor-shaped appearance of the expanded tentacle ends.

Holotype (Fig. 628)

Dimensions: Maximum dimension is 13.6 cm. A branch of a colony.

Locality: Jewell Reef, collecting station 66.

Depth: 12 m.

Collector: J.E.N. Veron.

Holotype: British Museum (Natural History).

Figs. 635, 636 *Catalaphyllia jardinei* (× 2.5).

Fig. 635 From Jervis Reef, same corallum as Fig. 632.
Fig. 636 From Great Palm Island.

Fig. 635 ▼

Fig. 636 ▼

Paratypes

Australian Institute of Marine Science.
Queensland Museum, Australia.

Distribution

Known only from the Great Barrier Reef as the present species distinct from the subgenus.

GENUS *CATALAPHYLLIA* WELLS, 1971

Generic synonymy

Catalaphyllia Wells, 1971a.

Type species *Pectinia jardinei* Saville-Kent, 1893. This is a redesignation of the type species by the author of the genus.[1]

Characters

This is a monospecific genus closely related to *Euphyllia.* It is primarily distinguished by the morphology of the polyps which are very different from the *Euphyllia* species described above.

Catalaphyllia jardinei (Saville-Kent, 1893)

Synonymy

Pectinia jardinei Saville-Kent, 1893.

Flabellum multifore Gardiner, 1904; Faustino (1927); *pars* Matthai (1928); (as *F. rubrum multifore*) Squires (1958); Chevalier (1971).

Euphyllia picteti Bedot, 1907; Matthai (1928); Yabe, Sugiyama & Eguchi (1936); Ma (1937); Eguchi (1938); Wells (1955a); Ma (1959); Nemenzo (1960).

Flabellum vacuum Crossland, 1952.

Catalaphyllia plicata (Edwards & Haime); Wells (1971a).

In his original description, Wells referred this species to *Rhipidogyra plicata* Edwards & Haime (figured by Matthai, 1928, Pl. XLI, Fig. 1). This specimen, however, belongs to the *Euphyllia* (*Fimbriaphyllia*) group of species and lacks the distinctive characters of *Catalaphyllia* noted under 'affinities' below. The next available name is *jardinei* of Saville-Kent who, in giving a description of the polyp, leaves no doubt as to the identity of his species.

Material studied

Jervis Reef, Lizard Island (4 specimens), **Palm Islands** (8 specimens), W of **Bowl Reef, Whitsunday Islands** (6 specimens), **Wistari Reef.**

These localities include collecting stations 43, 46, 55, 97, 102, 119.

Previous records from Eastern Australia

Warrior Reef, Thursday Island, Albany Passage (as *Pectinia jardinei*) Saville-Kent (1893); **Warrior Reef** (as *Euphyllia picteti*) Bedot (1907); **Port Newry** (as *Euphyllia picteti*) Wells (1955a); **Thursday Island** to **Port Newry** (as *Catalaphyllia plicata*) Wells (1971a).

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[1] Note on the Type Species of *Catalaphyllia*
In the original description of the genus *Catalaphyllia,* I made the erroneous assumption that *Euphyllia plicata* (Edwards & Haime, 1848b) was identical to two other species considered as junior synonyms of *E. plicata* (*Pectinia jardinei* Saville-Kent 1893 and *Flabellum multifore* Gardiner 1904). Therefore the next available name for the type species is Saville-Kent's *P. jardinei* = *Catalaphyllia jardinei* (S.K.) - J.W. Wells.

Characters

Colonies are free-living, initially monocentric and flabelloid (Figs. 629-634). Larger colonies develop a crescentic then flabello-meandroid form with a dome-shaped upper surface. They seldom exceed 20 cm diameter although colonies >1 m diameter are sometimes found. Valleys are very irregular but seldom >30 mm in width. They are very sinuous and frequently very long with few branches. Even in large coralla, the valleys usually form a single, continuous unit. Septa are usually irregular in size and appearance although in some coralla they appear to be arranged into 3 or 4 orders. They are slightly, unevenly, exsert. They may have dentate and/or finely serrated margins, especially their inner margins where elongate dentations may form weak trabecular columellae. Frequently, they are folded along the valley axis to form discontinuous laminar columellae. In small coralla it is usual for septa of higher orders to be more dentate than lower ones and the columellae to be better developed. Septa usually have finely granulated sides. The edge zone is usually narrow (<4 mm) and the exotheca finely costate. The endotheca is coarsely vesicular.

The appearance of the living polyps is very distinctive (Figs. 830, 831). They are large and fleshy with grey tentacles and striated green oral discs. Stomodaea are very large and prominent. Polyps are usually expanded day and night although at irregular intervals the tentacles contract and become flaccid. Sometimes they become greatly inflated except for the tips, which remain knob-like, usually purple or pink in colour.

Affinities

The growth form of *C. jardinei* is similar to that of *Euphyllia* (*Fimbriaphyllia*) species. Coralla are distinguished by having V-shaped open valleys with relatively

Fig. 637 *Catalaphyllia jardinei* from the Palm Islands with tentacles extended during the day.

straight-sided septa. These are less exsert than in *Euphyllia* species. *Euphyllia* are seldom free-living whilst *C. jardinei* is almost always free living. However, the primary difference between these genera is in the structure of the polyps, all of which are figured in the present account.

GENUS *PLEROGYRA* EDWARDS & HAIME, 1848

Generic synonymy

Plerogyra Edwards & Haime, 1848c; Matthai (1928); Chevalier (1975).

Type species *Plerogyra laxa* Edwards & Haime, 1848b.

Characters

Colonies are phaceloid, flabelloid or flabello-meandroid. The exotheca is cellular and covers the surface of the whole corallum. Corallite walls are parathecal. Septa are large, very exsert and widely spaced.

All east Australian *Plerogyra* are included in a single species, *P. sinuosa.* A second species, *P. simplex* Rehberg, 1892 (Fig. 644), known to occur in New Caledonia (Chevalier, 1975, as *P. taisnei*), eastern New Guinea (Louisiade Archipelago), New Ireland (Rehberg, 1892) and the Philippines has not been found on the Great Barrier Reef, although it might be expected to occur there on biogeographic grounds.

Plerogyra sinuosa (Dana, 1846)

Synonymy (partly after Matthai, 1928)

Euphyllia sinuosa Dana, 1846.

Euphyllia cultrifera Dana, 1846.

Plerogyra laxa Edwards & Haime, 1848b; Edwards & Haime (1857); Studer (1880); Ortmann (1888); Ma (1959).

Plerogyra excavata Edwards & Haime, 1848b; Edwards & Haime (1857).

Plerogyra sinuosa (Dana); Matthai (1928); Yabe, Sugiyama & Eguchi (1936); Searle (1956); Ma (1959); Pichon (1964); Scheer (1967, 1972); Chevalier (1971); Scheer & Pillai (1974); Pillai & Scheer (1974).

Material studied

Bramble Cay, Darnley Island (2 specimens), **Big Mary Reef** (5 specimens), **Yorke Island** (6 specimens), **Warrior Reef, Turtle Backed Island, Murray Islands** (4 specimens), barrier reef E of **Murray Islands, Aureed Island** (2 specimens), **Jewell Reef, Bewick Island** (2 specimens), **Lizard Island** (3 specimens), **Palm Islands** (10 specimens), **Pandora Reef, Lodestone Reef, Whitsunday Islands** (11 specimens), **Parker Reef, Swain Reefs** (2 specimens), **Heron Island, Wistari Reef.**

These localities include collecting stations 13, 27, 28, 29, 32, 33, 35, 36, 39, 66, 69, 81, 90, 95, 97, 98, 100, 102, 110, 111, 116, 117, 120, 125, 126, 128, 131, 133, 138, 140.

Figs. 638-641 *Plerogyra sinuosa,* Figs. 638-640 (× 0.5).

Fig. 638 From Aureed Island, collecting station 133.
Fig. 639 From Big Mary Reef, collecting station 131.
Fig. 640 From Bullumbooroo Bay, Great Palm Island, collecting station 35.
Fig. 641 From Hook Island, Whitsunday Islands, collecting station 39 (× 0.5).


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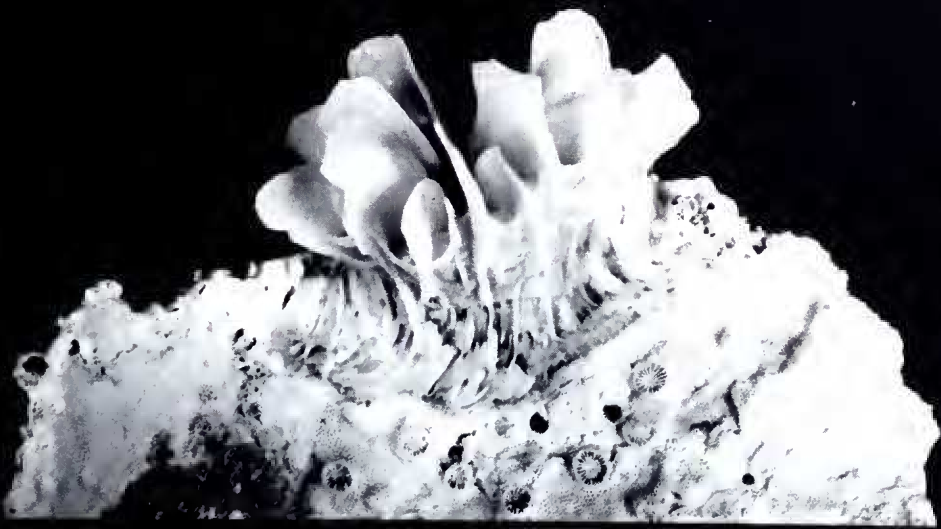
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Previous records from Eastern Australia

Cape York, Undine Reef, Bowen, Northumberland Islands (as *Plerogyra*) Wells (1955a).

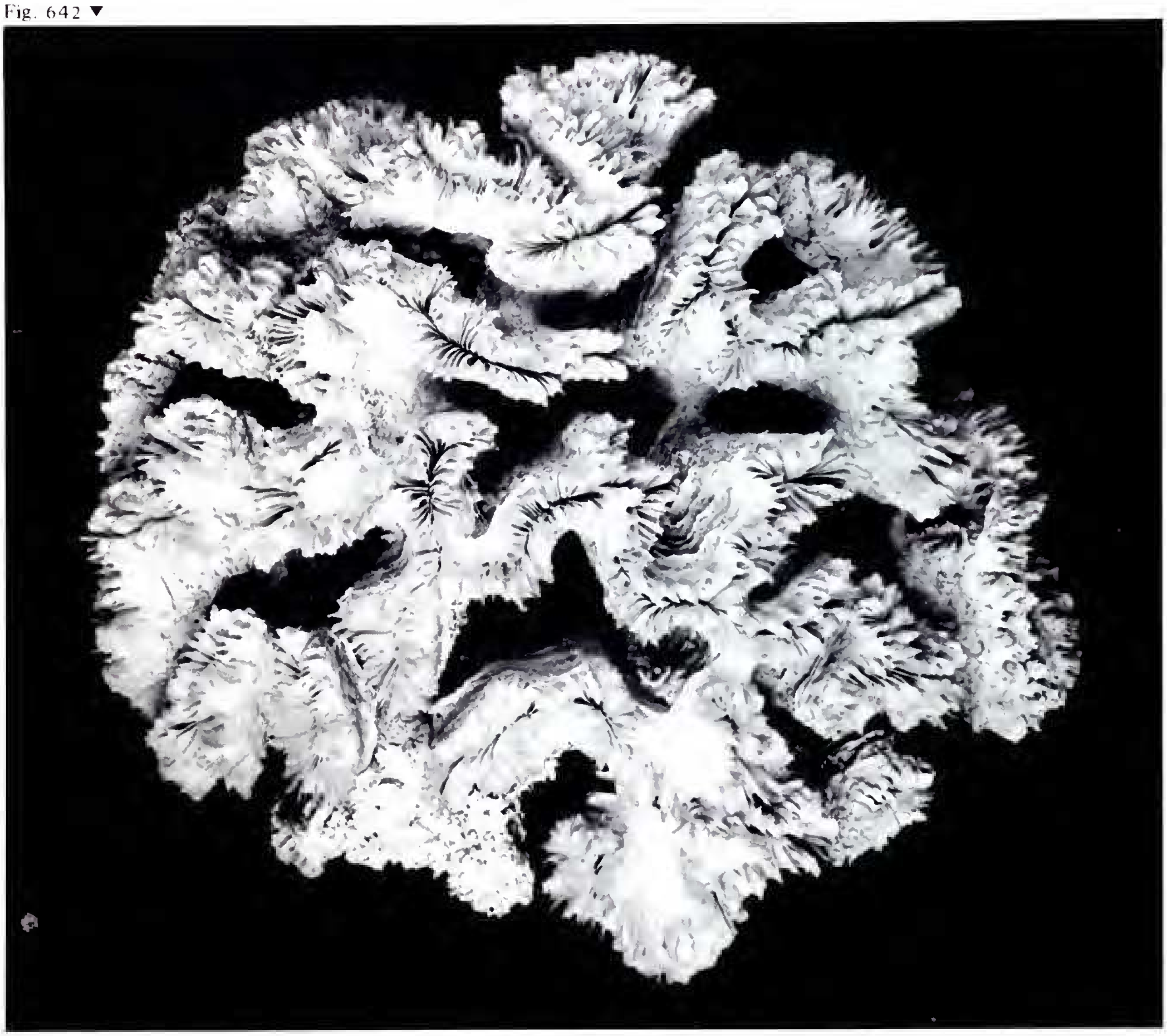
Characters

Juvenile coralla are monocentric, cylindrical, or more usually trochoid. These shapes may be maintained during subsequent growth with cylindrical colonies growing up to 30 cm long. Usually trochoid coralla became flabelloid then flabello-meandroid. In such cases the meanders may remain in contact but usually become separated into independent phaceloflabellate branches. In all cases, however, the colony has the shape of an inverted cone with a growing surface sometimes >1 m across.

Juvenile coralla have a hexameral symmetry with three markedly different septal cycles. This symmetry soon breaks down with the septa of larger coralla becoming increasingly irregular. Large corallites may have 4 or (rarely) 5 recognisable orders but more commonly orders cannot be distinguished. Septa show a remarkable range of size and shape. They may be up to 20 mm exsert, 35 mm broad, 2.5 mm thick. Adjacent septa frequently have markedly differing shapes giving coralla a ragged appearance. Margins are entire and usually smooth, inner margins are free and may be straight, twisted or folded in the direction of the valley axes. The sides of the septa may be smooth or weakly granulated. They never anastomose. In many coralla, the septa show a wide variety of abnormalities. Dissepiments may form on almost any part

Fig. 642 *Plerogyra sinuosa* from Hook Island, Whitsunday Islands, collecting station 39 (× 0·5)

Fig. 642 ▼



of the septa and these may give rise to one or more secondary septa with free inner margins. Some septa may be dentate, especially on their upper margins, where trabecular-like processes may form.

In small coralla the thecae are predominantly costate. In such cases the costae are well defined, markedly unequal and are frequently lobed, the lobes sometimes forming spines. These spines may become elongate and eventually develop into minute polyps. This method of budding may only be found in *Plerogyra* and *Euphyllia.* It does not occur in larger colonies as the costae become submerged in large, smooth dissepiments. As previously noted, dissepiments can form almost anywhere on the septa and contribute greatly to the ragged appearance of large coralla. Meanders with thick dissepimental thecae may be up to 6 cm across with the septa almost submerged. More usually, they are 2-4 cm across with septa markedly exsert. Columellae are not developed.

Living colonies are covered with large grey ectodermal vesicles similar to those described for *P. lichtensteini* (Figs. 643, 832-834). They differ in being larger (<2.5 cm diameter) and less readily retractable. They cover the larger septa during the day but are themselves covered by expanded tentacles at night.

This species is restricted to protected waters, preferring caves or crevices where it grows on vertical faces or overhangs. Large colonies are frequently found on flat substrates, in partially turbid water, along with other Eusmilliinae.

Distribution

Widely distributed through the tropical Indo-Pacific from the Red Sea to the Marshall Islands.

Fig. 643 *Plerogyra sinuosa* from Heron Island showing ectodermal vesicles with tentacles retracted during the day.

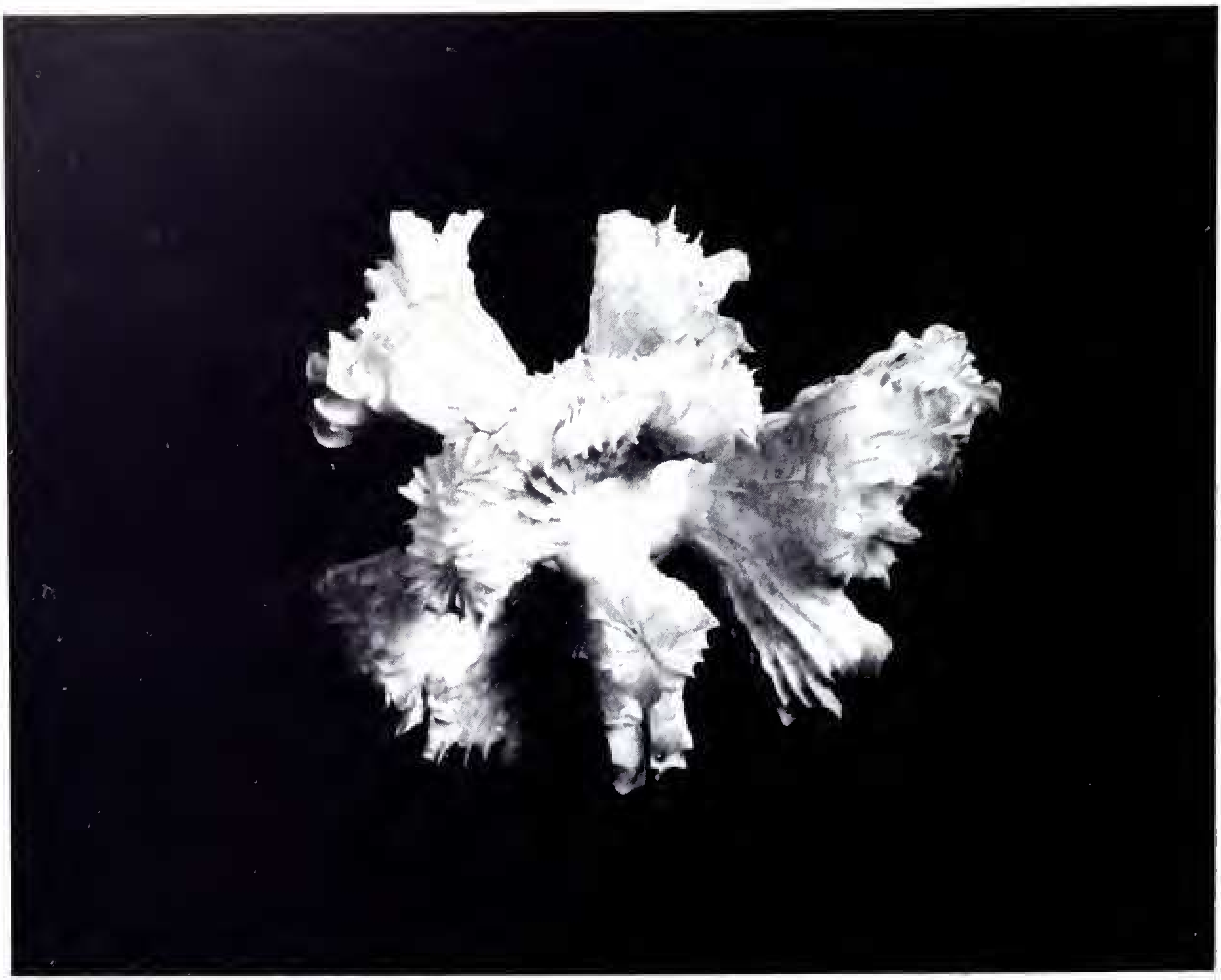


Fig. 644 *Plerogyra simplex* from Conflict Atoll, Louisiade Archipelago (× 0.7).

GENUS *PHYSOGYRA* QUELCH, 1884

Generic synonymy

Physogyra Quelch, 1884; Matthai (1928); Chevalier (1975).

Type species *Physogyra aperta* Quelch, 1884 = *Plerogyra lichtensteini* Edwards & Haime, 1851c.

Characters of the genus (after Vaughan & Wells, 1943)

Like *Plerogyra* but series closely united by walls; endothecal dissepiments highly vesicular.

Physogyra lichtensteini (Edwards & Haime, 1851)

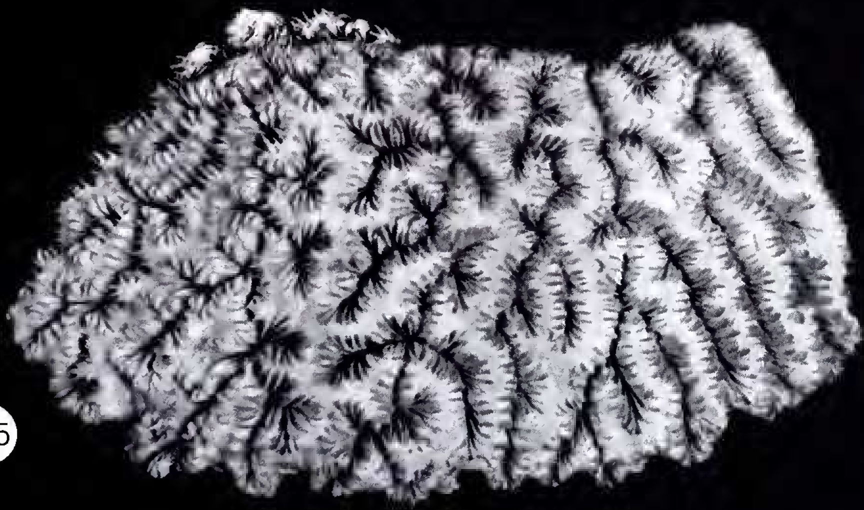
Synonymy

Plerogyra lichtensteini Edwards & Haime, 1851c; Edwards & Haime (1857).

Physogyra aperta Quelch, 1884; Quelch (1886).

Figs. 645-647 *Physogyra lichtensteini* (× 0.5).

Fig. 645 From Juno Bay, Fantome Island, Palm Islands, collecting station 43.
Fig. 646 From Parker Reef.
Fig. 647 From Jewell Reef.



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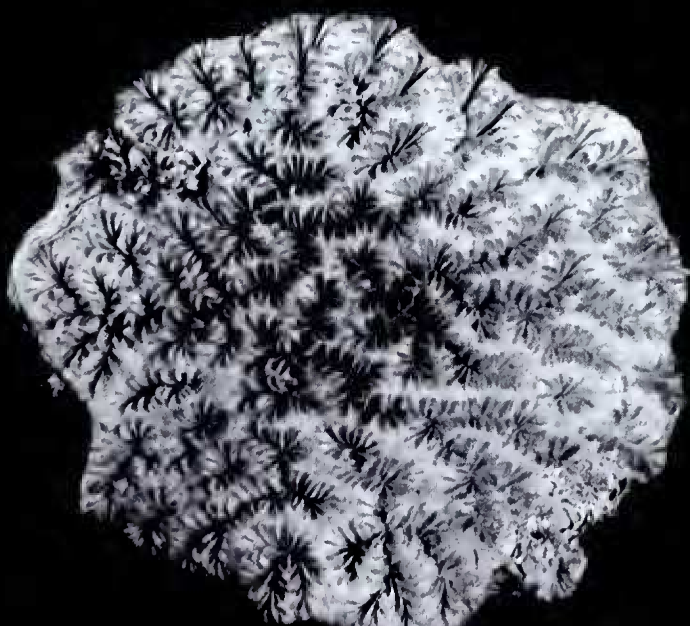

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Fig. 648 ▲


Fig. 649 ▲

Fig. 650 ▼


Fig. 651


Physogyra lichtensteini (Edwards & Haime); Matthai (1928); Yabe, Sugiyama & Eguchi (1936); Wells (1954); Ma (1959); Pichon (1964); Chevalier (1971).

Physogyra astraeiformis Umbgrove, 1940.

Quelch listed two species of *Physogyra*, *P. lichtensteini* and *P. aperta* to which Vaughan (1907b) added *P. gravieri* and *P. somaliensis* both from French Somaliland. Matthai (1928) considered all but the last of these synonymous. Chevalier (1971) reaffirmed the validity of *P. gravieri*, an opinion supported by the present study. The type specimen, as noted by Chevalier, has very shallow valleys, angular collines, thin septa which are not exsert and weakly developed columellae. *Physogyra somaliensis* is equally well distinguished by its narrower valleys and greater number of septa (8 per cm). Septa are often continuous between adjacent valleys, with a horizontal upper margin extending almost to the axis of the valleys. The endotheca is very abundant and highly vesicular.

Physogyra astraeiformis is characterised by monocentric or near monocentric corallites. It falls within the range of Great Barrier Reef *P. lichtensteini.*

Material studied

Anchor Cay, Darnley Island, Yorke Island, Ashmore Reef, Tijou Reef, Houghton Island, Jewell Reef, Lizard Island, plug reef near **Ribbon Reef, Palm**

Figs. 648-651 *Physogyra lichtensteini* (× 2.5).

Fig. 648, 649 From Juno Bay, Fantome Island, same corallum as Fig. 645.
Fig. 650 From Jewell Reef, same corallum as Fig. 647.
Fig. 651 From Parker reef, same corallum as Fig. 646.

Fig. 652 *Physogyra lichtensteini* from the Swain Reefs, showing tentacles expanded at night.

Islands (9 specimens), **Whitsunday Islands** (2 specimens), **Parker Reef, Swain Reefs** (2 specimens).

These localities include collecting stations 6, 13, 32, 37, 43, 57, 64, 69, 81, 91, 102, 106, 126, 129.

Previous records from Eastern Australia

Not previously recorded.

Characters

Colonies are flat or dome-shaped, frequently >1 m across and >30 cm thick. Their whole basal surface may be attached to the substrate or they may be raised on a stalk, the latter frequently being a result of erosion of basal skeletal material. Valleys may be long and sinuous or very short or a mixture of both. All skeletal structures are very large and simple. Septa are not arranged in orders. They are irregularly exsert up to 8 mm, are up to 18 mm wide, and extend to the valley midline where they may be curved, split or folded to form simplified axial elements. Septa of adjacent valleys are usually widely separated. Where they do meet they are usually interconnected by a high, thin ridge. Most septa are thin and delicate but some may be up to 3 mm thick near their base. Their inner margins are vertical or near vertical and only rarely are there any signs of dentations forming. There are no other ornamentations. Septa are joined by very large, thin, vesicular exothecal dissepiments, frequently up to 18 mm across. Gaps between the dissepiments may average as much as 3 mm giving such coralla extremely low densities. Viewed from above the dissepiments form large delicate blisters devoid of any ornamentation. There is no evidence of columellae although the inner margins of septa may be linked by fine developing dissepimental bars resembling trabeculae.

This species is common in protected habitats such as crevices and overhangs especially in turbid water with tidal currents. During the day, colonies have the appearance of a mass of small grey grape-like vesicles which obliterate the underlying skeleton (Fig. 835). Each vesicle overlies a septa, or occasionally, several septa. After mechanical interference the vesicles slowly contract and attain the appearance of a more usual epidermal layer. Elongate (up to 3 cm) tapering tentacles are expanded at night, largely obliterating the vesicles from view (Fig. 652). They arise from the rim of the valleys which is the level of the rim of the large oral discs. The mouths of polyps are large and well defined. Their position does not appear to correspond to any skeletal structure.

The function of the vesicles is not clear. They are traversed by fine folds suggesting the possible presence of ciliated tracts. Alternatively they may have a purely protective function.

Affinities

Both polyp and skeletal structures clearly distinguish this species from any others on the Great Barrier Reef. Juvenile monocentric coralla may resemble *Euphyllia* or *Plerogyra* species but this resemblance is clearly superficial and even juvenile colonies cannot be confused underwater.

Distribution

Widely distributed from Madagascar throughout the central Indo-Pacific east to the Marshall Islands.

XI
Family Dendrophylliidae Gray, 1847

The dendrophylliidae is composed of a wide assortment of mostly ahermatypic genera and of the three hermatypic genera *Turbinaria*, *Duncanopsammia* and *Heteropsammia*. Although the latter have completely different growth forms, they are clearly united by their highly porous, thick, synapticulothecal walls, their extensive, porous coenosteum and a septal arrangement which, at least in immature stages, is in accordance with Pourtalès plan.

GENUS *TURBINARIA* OKEN, 1815

Introduction

No study of *Turbinaria* can avoid constant reference to the detailed, methodical work of Bernard (1896), whose historical account (pp. 2-9) clearly summarises the findings and opinions of the earlier workers and serves as an introduction to his own treatment of the genus. In historical perspective, however, the work of Bernard is clearly associated with his predecessors who had little idea of intraspecific variability and it must now be recognised that his work has little value other than to be a well illustrated catalogue of specimens accompanied by notes on their morphology, history and occurrence.

Most of the earlier coral taxonomists have made reference to *Turbinaria* species grouped in varying ways under various other genera. Up to and including the time of Bernard, these specific names were applied to small numbers of similar specimens. With each successive study new names were given to specimens showing any significant deviations from older types. Bernard described some 58 species and today there are over 80 nominal species excluding pre-Bernard synonyms. Yet there has never been any major revision of the genus nor even a detailed study of the growth form variation and synonymy of any *Turbinaria* species.

The species descriptions resulting from this study differ greatly from those of previous authors. Most *Turbinaria* species from eastern Australia show a range of growth form which is paralleled by few other scleractinian genera. This variation has been (and can only be) determined by extensive underwater studies. It is emphasised, however, that this study has a primarily regional significance. Although some of the oldest specific names have been given to eastern Australian species, several such regional studies will have to be made before the taxonomy of the genus as a whole can be stabilised and its full diversity appreciated.

A total of 37 nominal species of *Turbinaria* have been recorded from Australia, 32 from the Great Barrier Reef. The type localities of 23 species are Australian, 17 of these are in the Great Barrier Reef. The *Turbinaria* of eastern Australia, therefore, make up a substantial proportion of the total Indo-Pacific complex of species. It is on these species, especially those with type localities from the Great Barrier Reef, that the following account is concentrated.

Generic Synonymy

Turbinaria Oken, 1815; (*pars*) Ehrenberg (1834); Edwards & Haime (1851c); Bernard (1896).

Explanaria Lamarck, 1816 (*pars*); (*pars*) Schweigger (1820); (*pars*) Ehrenberg (1832).

Gemmipora de Blainville, 1830; Dana (1846).

Type species *Madrepora crater* Pallas, 1766.

Characters of the genus (partly after Wells, 1956)

Colonies are hermatypic, large explanate, crateriform, contorted or foliaceous. Corallites are united nearly to the summits by an extensive coenosteum and have porous synapticulothecate walls. Pourtalès plan is apparent only in early stages. The columella is usually well developed.

Taxonomic history

As Bernard (1896) gave a detailed early history of the genus, only those aspects affecting modern taxonomy are summarised here. The name *Turbinaria* was given by Oken (1815) but not adopted by Lamarck (1816) who, under the genus *Explanaria*, grouped *Madrepora crater* Pallas (re-named *Explanaria infundibulum*) and *Madrepora cinerascens* Ellis & Solander (as *Explanaria mesenterina*) with 4 non *Turbinaria* species. Two true *Turbinaria* species, *T. palifera* and *T. stellulata*, were included in his *Astraea*. In 1820, Schweigger adopted Lamarck's *Explanaria* but used the older names *E. crater* and *E. cinerascens*. In 1830 de Blainville replaced *Explanaria* with *Gemmipora* and included in it *G. crater*, *G. mesenterina*, *G. peltata* (of Esper), *G. palifera* and *G. fungiformis* (new species).

Ehrenberg (1834) revived the named *Turbinaria*, composed partly of *Explanaria* Lamarck and partly of *Gemmipora* de Blainville and used this for small cup-shaped coralla to which he referred three species, *T. cupula*, *T. peltata* and *T. microstoma*. The genus *Explanaria* was retained for larger non cup-shaped specimens arranged into 7 species of which only one, *E. cinerascens*, is now recognised as a *Turbinaria*.

Dana (1848) readopted *Gemmipora* and included in it four old species, *G. peltata*, *G. crater*, *G. palifera* and *G. cinerascens* (which included Lamarck's *mesenterina* and Ehrenberg's *cupula* and *microstoma*) and three new ones, *G. patula*, *G. frondens* and *G. brassica*. The genus *Turbinaria* was finally adopted by Edwards & Haime (1851c). They included all Dana's species in it, along with *T. mesenterina* (as distinct from *T. cinerascens*) and de Blainville's *T. stellulata*.

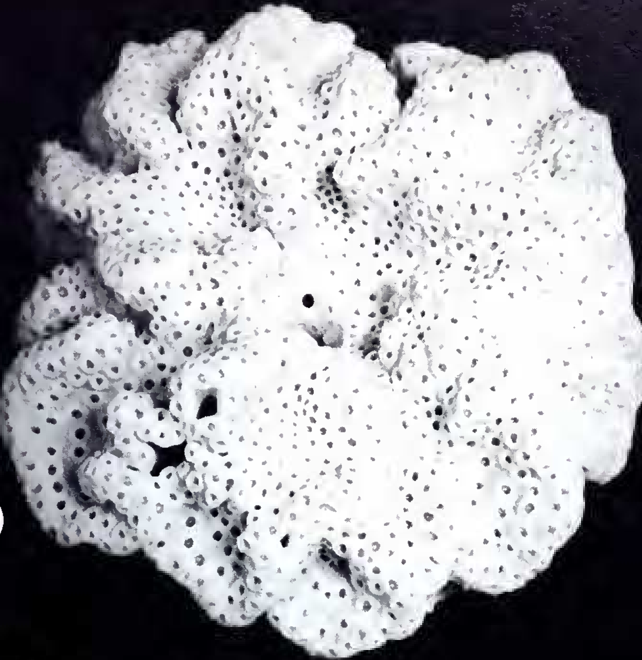
The contribution of subsequent authors has mostly been in the addition of new species. Bernard alone recorded 33 species from Australia. Of these Vaughan (1918) commented, 'How many of the 27 [*sic*] reputed species should be recognised as valid can only be determined by a critical revision of Bernard's original specimens, perhaps in the light of larger collections. Although Bernard did excellent work on the morphology of the coral skeleton (in fact his work is of fundamental importance), he seems never to have been able to group his specimens into what is understood by systematists as species'. Again, in 1954 Wells wrote 'the species of this genus require a thorough revision, and as Vaughan (1918, p. 148) has remarked, many of Bernard's species are largely based upon growth form and are of doubtful validity. For the present, however, I have based my identifications of Marshall Islands species of *Turbinaria* on Bernard's classification, admittedly an unsatisfactory and provisional treatment'.

There have been no further attempts to study *Turbinaria* other than by Nemenzo

Figs. 653-656 *Turbinaria peltata* (× 0.4).

Fig. 653 From Happy Bay, Long Island, Whitsunday Islands, collecting station 102.
Fig. 654 From Bewick Island.
Fig. 655 From Wistari reef, collecting station 117.
Fig. 656 From Jewell Reef.

653



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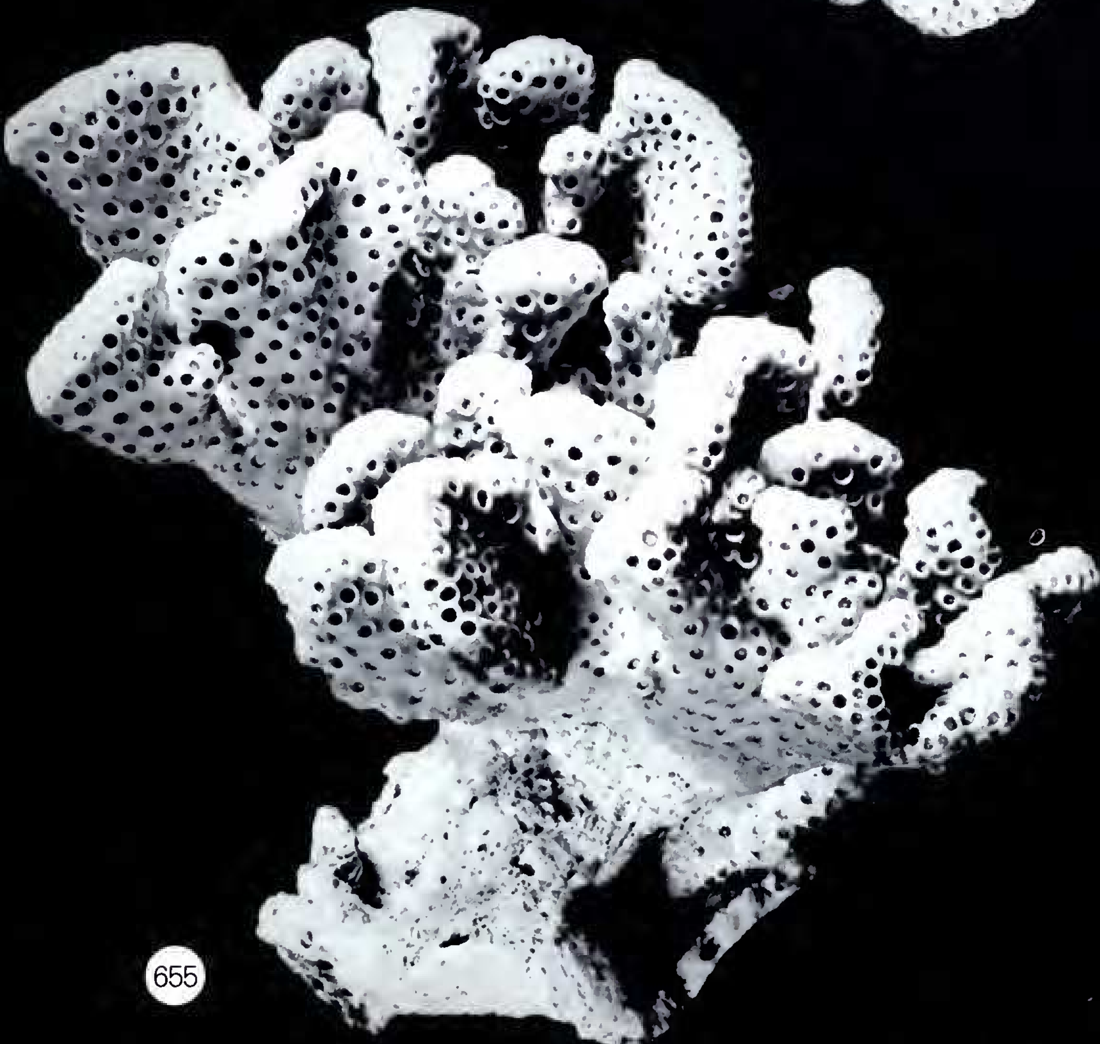

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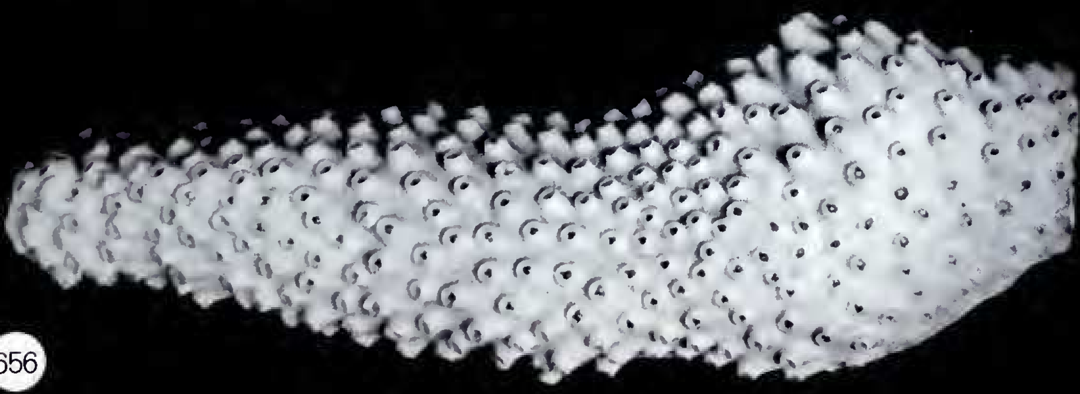


656

(1971) who, from Bernard, described the few specimens in his collection as well as a new species (*T. carinata*) from a single specimen which 'somewhat resembles *T. tubifera*'.

The present study indicates that at least nine true *Turbinaria* species occur along the east Australian coast. Of these, only one has been described recently (*T. heronensis* Wells, 1958), and of the remainder, only two (*T. reniformis* Bernard and *T. radicalis* Bernard) have not been attributable to pre-Bernard species names. However, the oldest and most frequently used name, *T. crater* Pallas, has not been used in the present account. Previous authors have generally applied the name *T. crater* to crateriform coralla with small, regular, outwardly inclined corallites, but, as noted by Bernard (p. 23), immature coralla of most *Turbinaria* species are crateriform, so that the name *crater* 'has been given to young examples of many different species'. The present collection contains many such coralla, most of which belong to other species, especially *T. frondens*, *T. mesenterina* and *T. reniformis* and underwater, *crater*-like colonies can invariably be linked to nearby mature colonies of these species. For this reason and because there is no type specimen nor adequate original description, the name *T. crater* cannot be conclusively given to any of the present species. This does not preclude the possibility that the name is applicable to some non-east Australian species.

Not all *Turbinaria* in the present collections have been satisfactorily identified. This is largely because most *Turbinaria* species lack conservative skeletal characters and have wide variation both in growth form and in calicular structures. Most of the unidentified coralla are either immature, *T. crater*-like coralla (referred to above) or *T. stellulata*-like coralla. In the latter case there is much regional variation within the Great Barrier Reef which suggests that either sibling species or geographic subspecies may be involved (see p. 399).

Turbinaria peltata (Esper, 1794)

Synonymy

Madrepora peltata Esper, 1794.

Gemmipora peltata (Esper), de Blainville (1834); Dana (1846).

Turbinaria peltata (Esper), Edwards & Haime (1860); Studer (1880); Quelch (1886); Ortmann (1889); Rehberg (1892); Bernard (1896); Bedot (1907); Folkeson (1919); Matthai (1923a); Faustino (1927); Gravely (1927); Eguchi (1938); (*pars*) Yabe & Sugiyama (1941); Crossland (1952); Wells (1955b); Searle (1956); Ma (1959); Nemenzo (1962); Utinomi (1965, 1971); Scheer & Pillai (1974).

Turbinaria dichotoma Verrill, 1871.

Turbinaria maxima Ortmann, 1888.

Ortmann (1888) gave a brief description of his *T. maxima* which (as noted by Bernard, 1896, partly as *T. marima*) appears to belong to *T. peltata*. Dana himself doubted the validity of his *T. patula* as separate from *T. peltata*, and also suggested that Ehrenberg's *T. cupula* was the same.

Material studied

Bramble Cay, Murray Islands, Warrior Reef, Yorke Island, Warrior Island, Turtle Backed Island (2 specimens), **Jervis Reef** (4 specimens), **Thursday Island, Bewick Island** (2 specimens), **Jewell Reef, Lizard Island** (3 specimens), **Low Isles, Palm Islands** (22 specimens), **Pandora Reef, Keeper Reef, Magnetic Island,**

Figs. 657-660 *Turbinaria peltata*, Figs. 657, 658 (× 2.5), Figs. 659, 660 (× 5.0).

Figs. 657, 659 Same corallum from Thursday Island, collecting station 53.
Figs. 658, 660 Same corallum as Fig. 654.

. 657 ▲

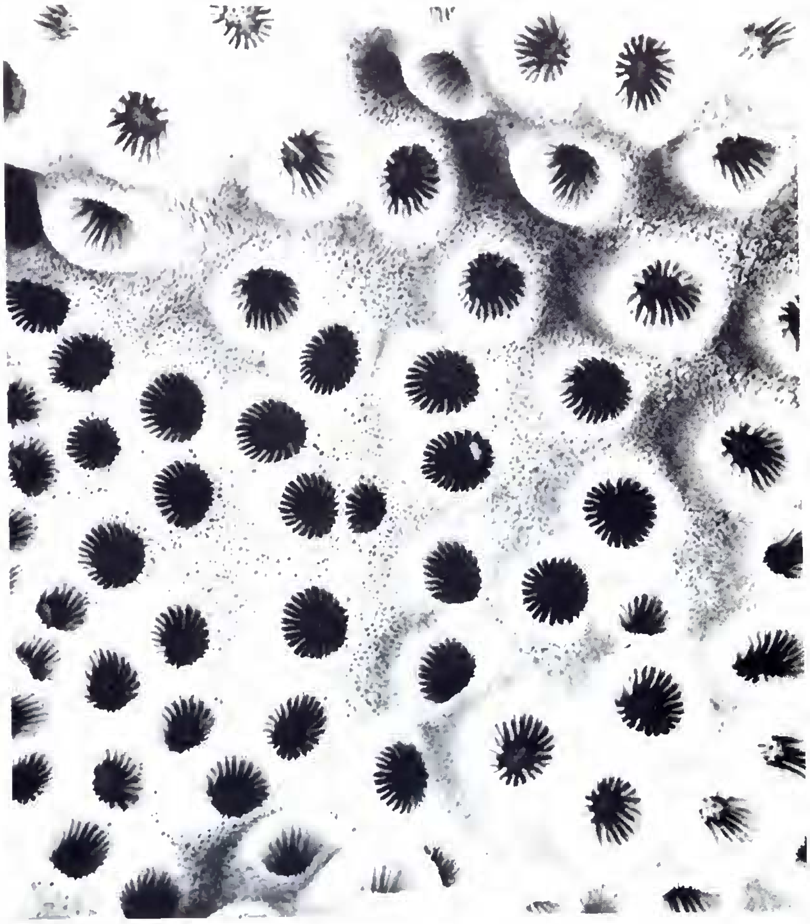


Fig. 658 ▲

Fig. 659 ▼

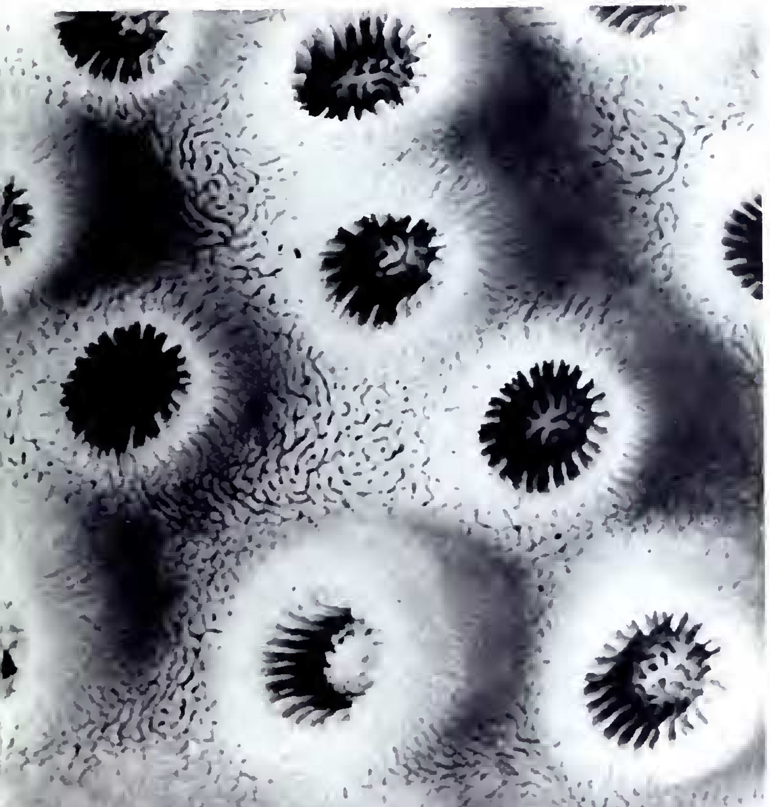


Fig. 660 ▼

Whitsunday Islands (12 specimens), **Swain Reefs, Frigate Cay, Masthead Island, Heron Island, Wistari Reef** (3 specimens), **Solitary Islands, Lord Howe Island** (2 specimens).

These localities include collecting stations 12, 13, 28, 32, 34, 38, 41, 43, 45, 53, 55, 57, 58, 60, 69, 81, 91, 93, 94, 98, 100, 101, 102, 111, 116, 119, 120, 121, 128, 138, 147.

Previous records from Eastern Australia

Torres Strait, Bernard (1896); **Low Isles,** Crossland (1952), Stephenson & Wells (1955); **Heron Island,** Salter (1954); **Moreton Bay,** Wells (1955a); **Solitary Islands,** Veron *et al.* (1974); **Lord Howe Island,** Veron (1974), Veron & Done (1979).

Characters

Most small colonies consist of horizontal plates which may adhere closely to the substrate or else are raised on stalks which are devoid of corallites. This growth form may continue till colonies reach many metres in diameter, with laminae remaining encrusting or tabular (Fig. 837). They become greatly thickened, but remain unifacial. Many coralla develop irregularities on their upper surface which develop into ridges with budding margins and these develop into bifacial fronds or into cylindrical columns (Fig. 838).

Corallites may be crowded or widely spaced, flush with the coenenchyme or protruded up to 2.5 cm. As with other *Turbinaria* species, corallites tend to protrude more on convex surfaces. Frequently they are inclined towards the corallum margins which are mostly composed of closely packed, outwardly projecting corallites produced by extra-tentacular budding. With subsequent growth they become upwardly projecting and increasingly immersed in coenosteum. Thus, the density of corallites in flat coralla usually decreases toward the corallum centre. In foliaceous colonies, budding mostly occurs on the upper margins of the fronds and there is little tendency for fronds to anastomose.

Calices are mostly circular, averaging 3-5 mm diameter. Septa are ranged in 3 orders, the first two being similar except at their inner margins where there is a slight but regular alternation. They project inwards $\frac{1}{4}$ to $\frac{1}{2}$ the calice radius. The third cycle is greatly reduced or sometimes absent. All septa are granulated. The columellae lie deep within the calices. They are dome shaped and spongy, usually with a foliaceous appearance. In some coralla the columellae have a compact, directive ridge or central plate, to which the rest of the columella loosely adheres. The exotheca and coenosteum have a spongy appearance with the skeletal elements arranged irregularly or in fine, striate ridges.

Living colonies frequently have their polyps extended during the day (Figs. 839, 840). Tentacles are thick and up to 1 cm long. The colour of the polyps appears to vary geographically. At Lord Howe Island they are white, throughout most of the Great Barrier Reef they are mostly pale brown but are sometimes bright yellow. When the polyps are retracted, colonies are usually a pale, milky brown. Large colonies are most frequently found in relatively deep water and the species mostly favours turbid, non reefal, biotopes.

Figs. 661-663 *Turbinaria peltata, in situ.*

Fig. 661 From the Swain Reefs.
Fig. 662 From Heron Island.
Fig. 663 From Lord Howe Island, collecting station 147, showing tentacles extended during the day.

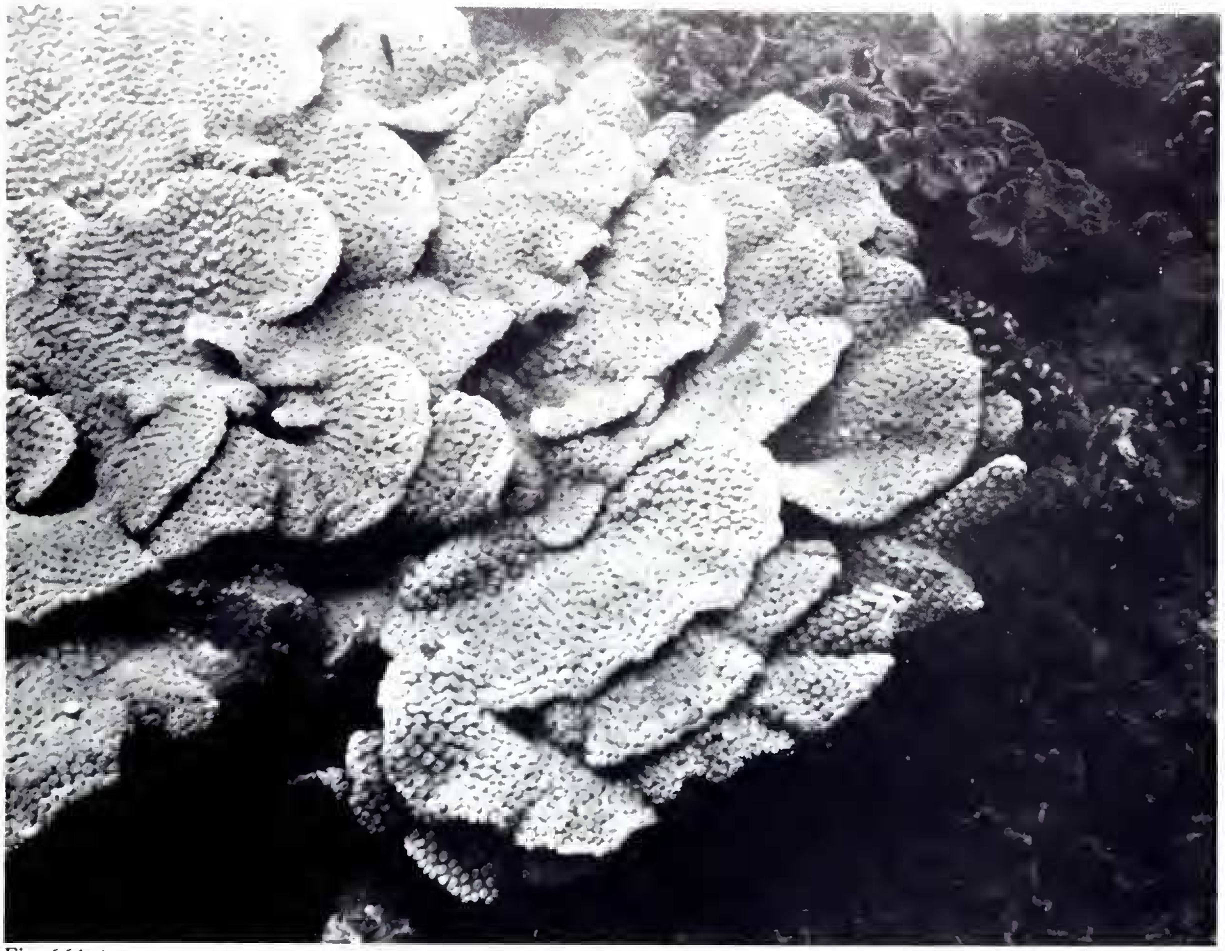
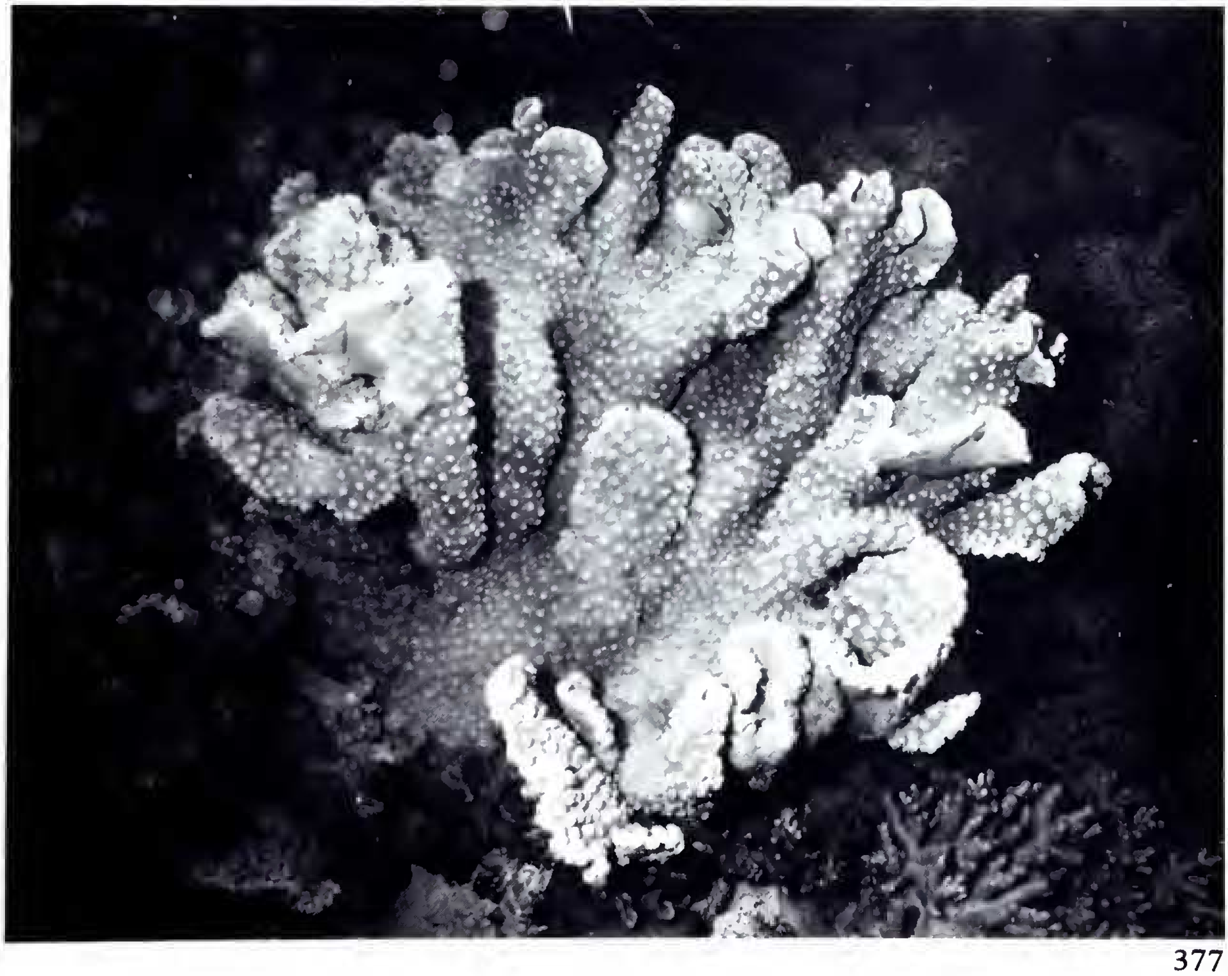


Fig. 661 ▲

Fig. 662 ▼


Affinities

The large size of the corallites and the marginal budding (as described above) clearly separated *T. peltata* from other Great Barrier Reef *Turbinaria* and it appears that this species remains thus distinct through its full geographic range. Similarities with *T. patula* are discussed below (p. 381).

Distribution

Widely distributed from east Africa to Japan, the Marshall Islands and Fiji and ranges far into northern and southern temperate waters.

Turbinaria patula (Dana, 1846)

Synonymy

Gemmipora patula Dana, 1846

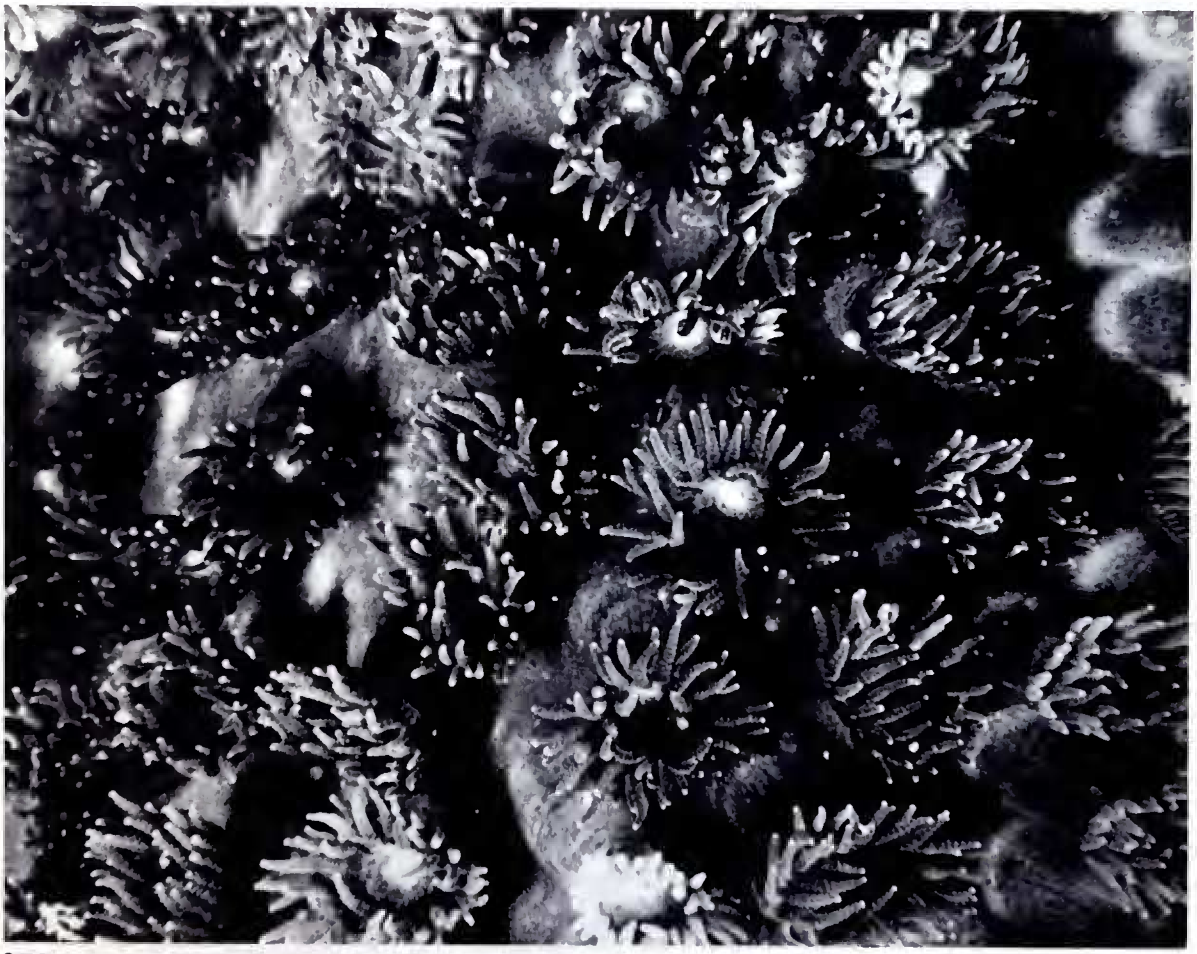
Turbinaria patula (Dana); Quelch (1886); Bernard (1896).

?*Turbinaria robusta* Bernard, 1896.

Bernard added ?*T. fungiformis* Michelin, 1840 and *T. bankae* Giebel, 1861 to his synonymy of *T. patula* although he doubted the latter's validity: 'although corals are included under it which differ sufficiently from *T. peltata*, they are connected with that type by numerous transition forms'. Bernard's collection of *T. patula* in the British Museum is a mixture of *T. patula* and *T. peltata*. Dana himself also doubted the validity of *T. patula*, claiming that it may be the same as *T. peltata*. The holotype appears to have been lost, but Dana's description agrees well with the present species.

Turbinaria robusta (holotype from Port Denison) may be a shallow water growth form of this species although no coralla in the present series have such a convoluted margin.

Fig. 663 ▼



Material studied

Thursday Island, Lizard Island (2 specimens), **Palm Islands, Whitsunday Islands, Swain Reefs** (2 specimens), **Heron Island** (5 specimens), **Wistari Reef** (9 specimens), **Lord Howe Island** (2 specimens).

These localities include collecting stations 46, 54, 68, 69, 99, 102, 115, 116, 117, 147.

Previous records from Eastern Australia

Wednesday Island, Quelch (1886) (as *T. patula* and *T. robusta*) Bernard (1896); **Port Denison** (as *T. robusta*) Bernard (1896); unspecified localities in **Torres Strait** and **Great Barrier Reef,** Bernard (1896); **Lord Howe Island,** Veron & Done (1979).

Characters

Young colonies consist of horizontal plates on short stalks. With subsequent growth the plate edges become upturned and develop into large, irregularly folded, sub-vertical fronds. Corallites are large (4-6 mm diameter at their rim) and are strongly inclined towards the frond margins, often in irregular rows. On their distal side they may protrude up to 1.8 cm from the coenosteum while their proximal side remains submerged or only just protrudes. They are conical to tubular in shape with elliptical calices averaging 3.5 mm maximum diameter. The rims of most calices are slightly dentate as the upper edges of the unfused septal elements are slightly exsert. Septa are very short and wedge-shaped with fine, vertical inner margins. In most

Figs. 664, 665 *Turbinaria* cf. *patula* (× 0.33).

Fig. 664 From Lord Howe Island, collecting station 147.
Fig. 665 From Wistari Reef, collecting station 117, overlying *Turbinaria mesenterina.*

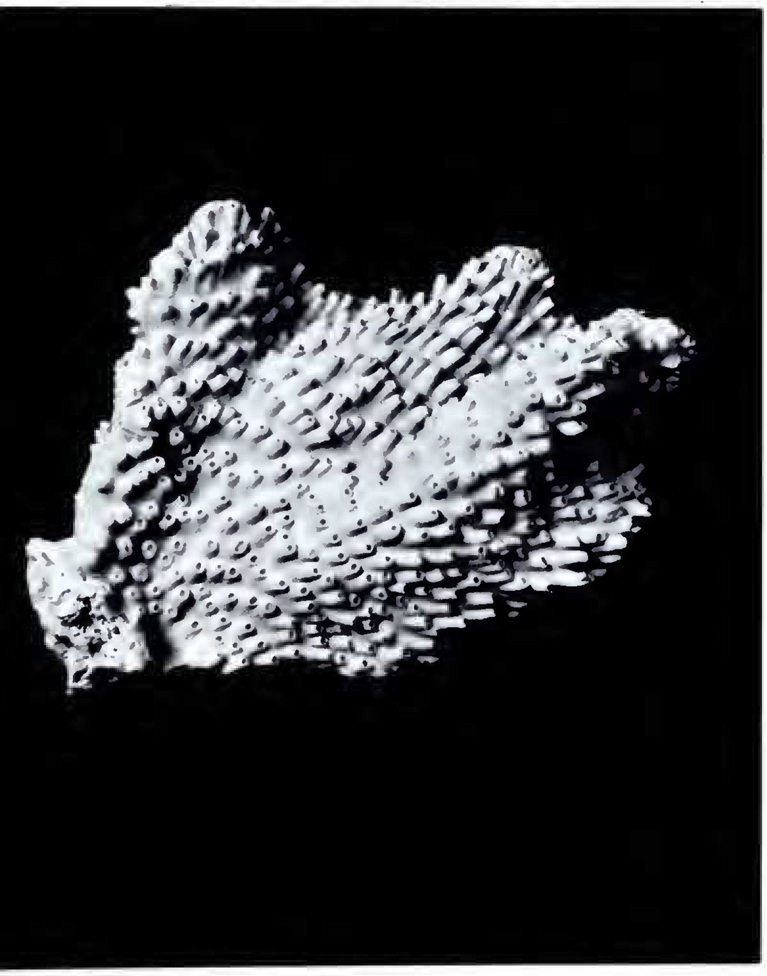


Fig. 666 ▲

Fig. 667 ▲

Fig. 668 ▼

Fig. 669 ▼

corallites at least one septum is abnormally large. Otherwise the septa are approximately equal. The columellae are very large, dome-shaped and spongy and occupy most of the calicular fossa. Frequently they are seen to be composed of fine, vertical lamellae, which may be crenellated or twisted. The coenosteum is usually relatively coarse.

Living colonies are pale brown or green in colour.

Skeletal variations

Although *T. patula* occurs throughout the Great Barrier Reef, it is nowhere common and has not been found in sufficient quantity to trace growth form changes underwater. All specimens of the present series are either horizontal plates or are composed of irregular sub-vertical folds. Such colonies may be over 1 m in height and several metres across.

Affinities

Turbinaria patula is closest to *T. peltata* but can hardly be confused with it. Figs. 665 and 655 illustrate two coralla that were growing next to each other on Wistari Reef. *Turbinaria peltata* has larger corallites with much larger calices which are not so strongly inclined. The septa of *T. peltata* are very distinctive, with the first two orders alternating and without the one or more abnormally large septa found in *T. patula*.

Turbinaria patula may also show some resemblance to *T. frondens*, which may have similar growth forms. It primarily differs in having relatively uniform corallites of larger size with much larger calices.

Distribution

Although this species has been recorded many times in the literature the only confirmed localities for it are northern and eastern Australia and Fiji.

Turbinaria frondens (Dana, 1846)

Synonymy

Gemmipora frondens Dana, 1846.

Turbinaria frondens (Dana); (as *T. frondescens*) Edwards & Haime (1860); Bernard (1896); ?Gravely (1927); Crossland (1952); Stephenson & Wells (1955); Nemenzo (1962).

?*Turbinaria danae* Bernard, 1896; Gardiner (1898); Wells (1955b); Ma (1959).

?*Turbinaria contorta* Bernard, 1896; Eguchi (1938, 1968); Yabe & Sugiyama (1941); Ma (1959); Utinomi (1965).

?*Turbinaria rugosa* Bernard, 1896; Yabe & Sugiyama (1941); Ma (1959); Eguchi (1968).

Turbinaria foliosa Bernard, 1896; Yabe & Sugiyama (1941); Nemenzo (1962).

Turbinaria pustulosa Bernard, 1896; Nemenzo (1962); (as *T. pustulosa*) Ma (1959).

Turbinaria magna Bernard, 1896; Ma (1959).

Turbinaria edwardsi Bernard, 1896; Ma (1959).

Turbinaria abnormalis Bernard, 1896.

Figs. 666-669 *Turbinaria patula* (× 2.5).

Fig. 666 From Lord Howe Island, same corallum as Fig. 664.
Fig. 667 From Bushy Island-Redbill Reef, collecting station 185.
Fig. 668 From Heron Island, collecting station 115.
Fig. 669 From Wistari Reef, same corallum as Fig. 665.

Turbinaria aurantiaca Bernard, 1896.

?*Turbinaria ramosa* Yabe & Sugiyama, 1941.

All except two of Bernard's species in the above synonymy have type specimens with approximately cylindrical corallites inclined on the lamina and numerous short septa with vertical inner margins and isodimensional, convex, columellae. The two exceptions are *T. contorta* (a single specimen from the South China Sea) and *T. rugosa* (two specimens from Taiwan) which have most corallites situated on conical protuberances and septa which have sloping, frequently anastomosing, inner margins and which are relatively few in number. In most other respects these nominal species are closest to *T. danae.* Other (non type) specimens attributed by Bernard to various of the above synonyms have less clear affinities, e.g. *T. pustulosa* from the Gulf of Carpentaria is closer to the holotype of *T. elegans* and *T. magna* from Torres Strait appears to be *T. reniformis.*

Turbinaria ramosa Yabe & Sugiyama from Japan is identical to some specimens of the present series (mostly from Lord Howe Island) which are characterised by the presence of very elongate corallites on the tops of convex or hillocky parts of laminae (Fig. 677). These specimens intergrade completely with *T. danae*-like specimens in the present collection. However, there remains some possibility that two species are involved: *T. frondens* and *T. danae,* the latter including *T. contorta, T. rugosa* and *T. ramosa.*

Six of the 9 species of Bernard which are here included in *T. frondens* have been recorded by him from Australia. Three of these, *T. aurantiaca, T. pustulosa* and *T. abnormalis,* have their type locality in the Great Barrier Reef, the first two from Port Denison, the last unspecified.

It is noteworthy that 4 of Bernard's 9 major subdivisions of *Turbinaria* are represented by this one species. Bernard himself noted that several of his species have certain points of resemblance to each other (and to other valid species). However, these are not discussed here; all species but *T. danae* and *T. magna* were described from 4 specimens or less and all without discussion of environmentally induced variability or habitats.

Material studied

Bramble Cay (2 specimens), **Anchor Cay** (2 specimens), **Campbell Island** (2 specimens), barrier reef E of **Murray Islands, Murray Islands, Turtle Backed Island** (2 specimens), **Tijou Reef, Lizard Island, Eyrie Reef, Ribbon Reef, Palm Islands** (9 specimens), **Pandora Reef** (4 specimens), **Magnetic Island** (6 specimens), **Bait Reef, Whitsunday Islands** (2 specimens), **Pompey Complex** (2 specimens), **Swain Reefs** (5 specimens), **Masthead Reef** (2 specimens), **Wistari Reef** (14 specimens), **Heron Island** (2 specimens), **Lord Howe Island** (3 specimens).

These localities include collecting stations 4, 5, 6, 10, 11, 20, 60, 75, 95, 134, 139, 140, 146, 149, 150, 154, 156, 161, 176, 181, 184, 185, 192, 220, 221, 222, 223, 224, 226, 228, 239, 252, 253, 261, 265, 266.

Figs. 670-673 *Turbinaria frondens,* Figs. 670-672 (× 0.5).

Fig. 670 From the Pompey Complex, collecting station 75.
Fig. 671 From Wistari Reef.
Fig. 672 From Juno Bay, Fantome Island, Palm Islands, collecting station 43.
Fig. 673 From Cateran Bay, Border Island, Whitsunday Islands, collecting station 101.

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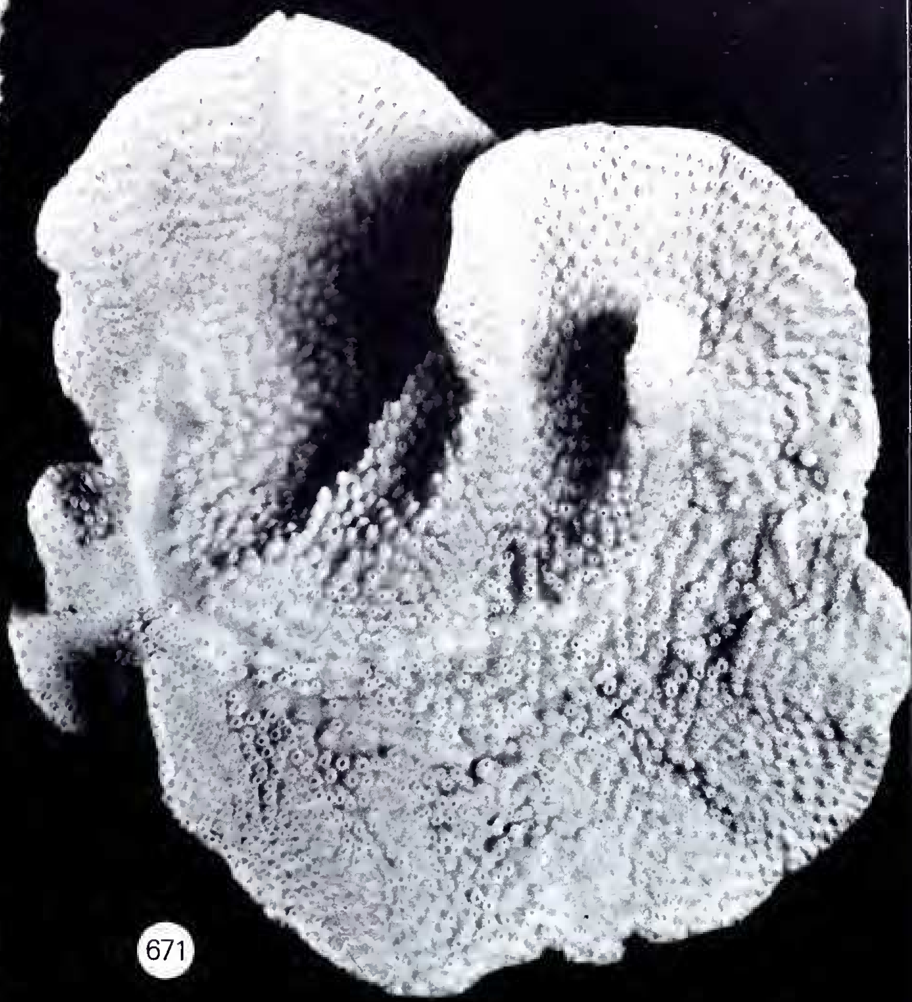

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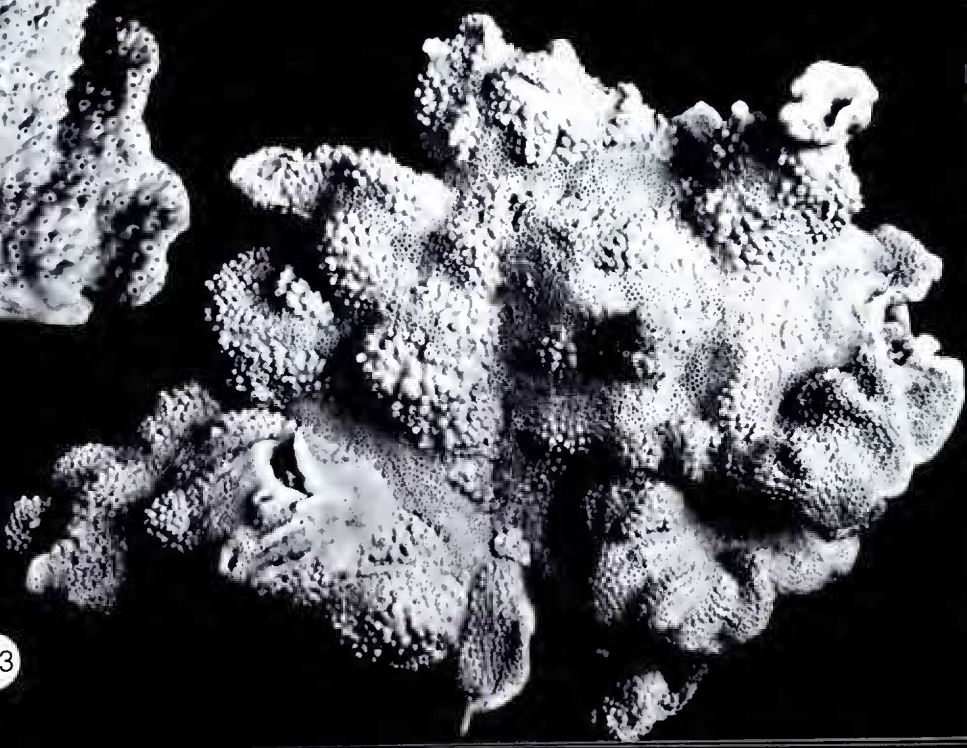

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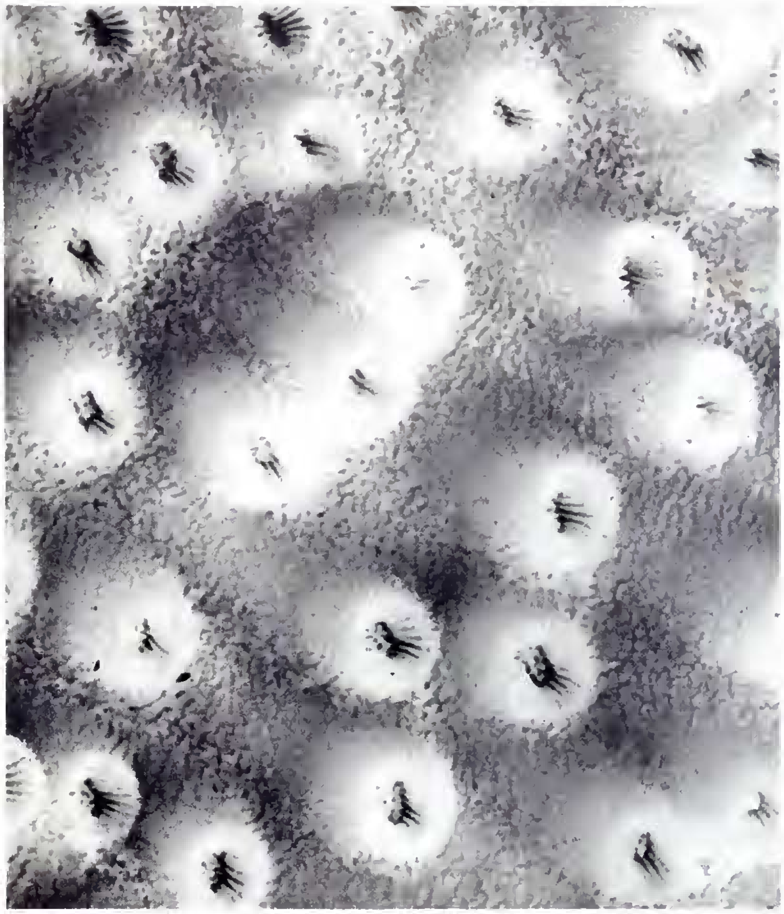

Fig. 674 ▲

Fig. 675 ▲

Fig. 676 ▼

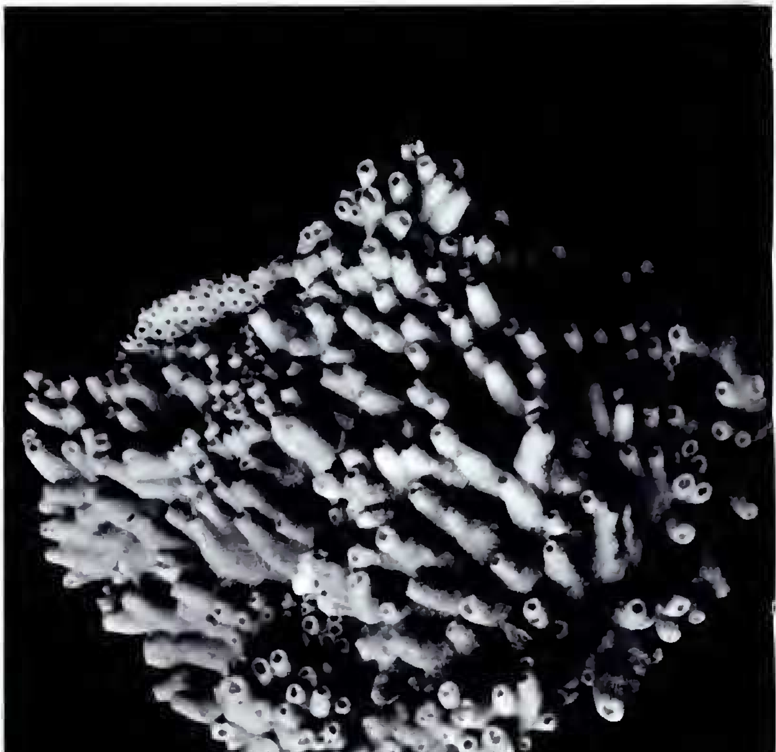

Fig. 677 ▼

Previous records from Eastern Australia

Torres Strait (as *T. magna*) Bernard (1896); **Low Isles,** Crossland (1952), Stephenson & Wells (1955); **Green Island** (as *T. magna*) Bernard (1896); **Port Denison** (as *T. aurantiaca, T. pustulosa, T. magna*) Bernard (1896); **Moreton Bay** (as *T. danae*) Wells (1955b); **Solitary Islands** (as *T. danae, T. frondens*) Veron *et al.* (1974); **Lord Howe Island** (as *T. danae*) Veron (1974), (as *T. frondens*) Veron & Done (1979); **Great Barrier Reef** (as *T. abnormalis*) Bernard (1896).

Characters

Colonies have encrusting, massive, columnar, crateriform or foliaceous growth forms. Some colonies may have only one of these growth forms, most commonly crateriform or foliaceous. Other colonies, especially larger ones (which may frequently exceed 4 m diameter), may be composed of composites of various of these forms (Fig. 847). It is this polymorphism which was the origin of Bernard's 9 junior synonyms. Large coralla, or those with irregular growth forms, are readily distinguished by the extreme variability of their corallites. Crateriform coralla, or those composed of regular fronds, are unifacial with regularly spaced corallites inclined towards the margins. Such corallites are regularly protuberant, conical in shape, and have circular apertures 1.5-2.5 mm diameter. They decrease in size at the margins where budding normally occurs. Where the corallum surface is irregular, however, corallites have circular apertures of 1-3 mm and may be up to 9 mm diameter at the base. They may be flush with the coenosteum or protrude up to 2.5 cm. On concave surfaces, corallites are usually small, crowded and become increasingly submerged in coenosteum until they have no definable thecae. On convex surfaces they may become very protuberant (Figs. 848, 849). However, areas of coenosteum devoid of corallites may occur in almost any position on irregular coralla and appear to reflect differential growth rates of the corallum surface.

Calicular structures are less variable. Septa are of one order, the number of which varies with the size of the corallites, but is usually 18-33. They are not exsert. They extend inwards $\frac{1}{4}$-$\frac{1}{3}$ the calice radius and usually have vertical or near vertical inner margins. All septa are granulated. Columellae may be rounded, spongy, hemispherical domes, especially in larger corallites with short septa, but in most corallites they are eliptical and usually have a directive ridge which may be plate-like. All septa reach the columellae well below their crests or ridges. The coenosteum has a fine spongy appearance which usually becomes finely striated or reticulated on the corallite walls.

Living colonies are usually dark brown to grey in colour, sometimes with green or reddish calices. The species occupies a wide range of habitats with large colonies usually occurring in partially turbid water.

Growth form variation and affinities

The affinities of *T. frondens* with other Indo-Pacific species are unclear, firstly because of the large number of nominal species involved and secondly because the present series contains a wide range of forms which show varying degrees of similarity with type specimens from other geographic regions. Thus, there is sometimes no clear distinction between what may be considered to be intra-specific geographic variation of *T. frondens* and what may be a separate species in another region.

Figs. 674-677 *Turbinaria frondens,* Figs. 674-678 (× 5.0).

Figs. 674, 675	From Wistari Reef, same corallum as Fig. 671.
Fig. 676	From Juno Bay, Fantome Island, same corallum as Fig. 672.
Fig. 677	From Lord Howe Island, showing close similarity with the holotype of *Turbinaria ramosa* (× 0.9).

Within the east Australian region, cup-shaped, vasiform or foliaceous coralla with regularly spaced corallites of uniform appearance are common throughout the Great Barrier Reef. These coralla intergrade with irregularly shaped coralla with irregularly spaced corallites of widely varying size and appearance. The latter form is uncommon on the Great Barrier Reef but is abundant at Lord Howe Island. Despite extensive field studies, the authors have not been able to establish criteria for separating these two groups as distinct species. Full ranges of intermediate forms have been observed within single biotopes and some large coralla have most of the range of corallite variation of the whole series.

Despite its intraspecific heterogeneity, *T. frondens* is normally readily separable from other east Australian *Turbinaria*. Coralla showing wide variation in corallite size and distribution do not resemble any other species. Coralla with uniform corallites are closest to *T. patula* at one extreme and *T. mesenterina* at the other. The corallites of *T. patula* are larger, have shorter septa and usually have one or more abnormally large septa. *Turbinaria mesenterina* usually has distincitve growth forms (see p. 391). Coralla from deeper water may have a similar growth form to those of *T. frondens* but are readily distinguished by their smaller corallites, with septa of irregular length, in 2 or 3 orders.

Distribution

Widely distributed in the western Pacific from Japan and the Philippines east to Fiji and ?Samoa, but apparently absent from the Indian Ocean.

Turbinaria mesenterina (Lamarck, 1816)

Synonymy

Explanaria mesenterina Lamarck, 1816.

Gemmipora mesenterina (Lamarck); de Blainville (1834).

Turbinaria mesenterina (Lamarck); Brüggemann (1879a); Klunzinger (1879); Ortmann (1888); Rehberg (1892); Bernard (1896); Gardiner (1898); Gravier (1911); Crossland (1941); Rossi (1954); Wells (1954); Pichon (1964); Scheer (1967); *non* Yabe & Sugiyama (1941).

Turbinaria tubifera Bernard, 1896; Matthai (1923a); Yabe & Sugiyama (1941); Ma (1959).

Turbinaria venusta Bernard, 1896; Ma (1959).

?*Turbinaria crassa* Bernard, 1896; Nemenzo (1962).

Turbinaria speciosa Bernard, 1896.

All of the above synonyms of *T. mesenterina* are species of Bernard, all except *T. tubifera* with their type localities in the Great Barrier Reef. Bernard's figured specimen of *T. mesenterina* has only slightly protuberant corallites which are not inclined on the corallum surface. The holotype of *T. tubifera* is similar to this specimen. The holotype of *T. venusta* has slightly protuberant, non-inclined corallites with distinct margins. That of *T. crassa* is a fragment of a thick frond with relatively small, non-protruding corallites. Columellae are large and occupy up to two-thirds the calice diameter.

Turbinaria tubifera and *T. venusta* clearly fall within the range of variation of the *T. mesenterina* described below. The positions of *T. crassa* and *T. speciosa* are less

Figs. 678-685 *Turbinaria mesenterina* (× 0.5).

Fig. 678	From Nymph Island.
Figs. 679, 682	From Geoffrey Bay, Magnetic Island.
Figs. 680, 681, 683-685	From Pandora Reef, collecting station 111.

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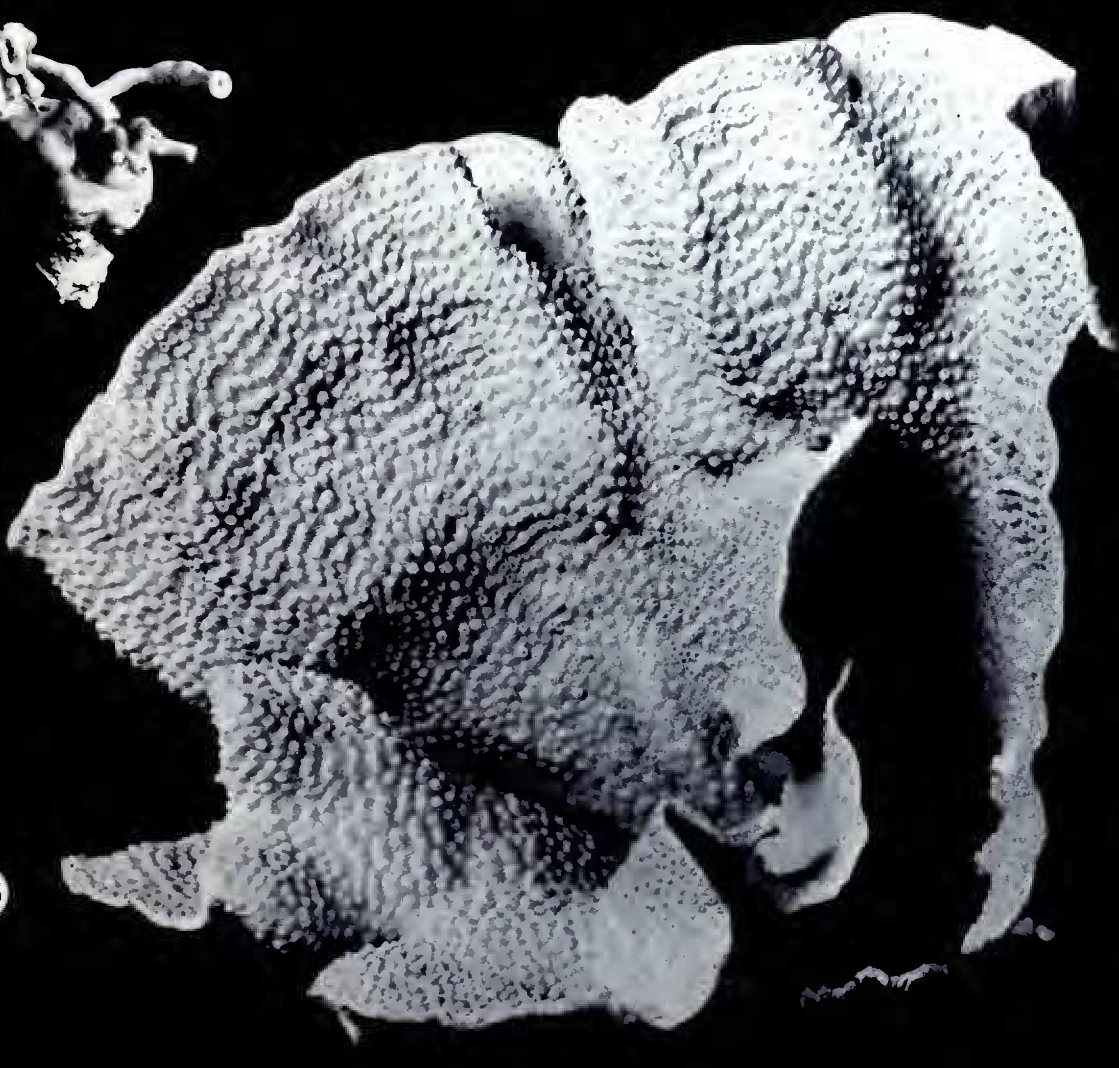
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clear. The single specimen attributed to *T. crassa* has a partly glomerate growth form resembling that of *T. elegans.*

The name *mesenterina* is used here in preference to *cinerascens* as the latter cannot be reliably identified from Ellis and Solander's figure and the type specimen is lost.[2] The historical usage of these names is documented by Bernard (1896) p.58. Similarly, *T. crater* Pallas may well be the same species, but cannot be identified with certainty (see p. 374). Lamarck's type of *T. mesenterina* from the Indian Ocean is a flat corallum with folded margins (approximately 12 x 12 cm). Corallites are similar to those of east Australian specimens described below except that the third cycle of septa is inconspicuous and the columellae are more rounded than elliptical and not very prominent.

Material studied

Anchor Cay, Campbell Islet, Big Mary Reef (2 specimens), **Yorke Island** (3 specimens), **Warrior Reef** (3 specimens), **Murray Islands** (9 specimens), **Turtle Backed Island, Aureed Island** (3 specimens), **Dungeness Reef, Newman Reef, Jervis Reef, Thursday Island, Bewick Island** (3 specimens), **Nymph Reef** (2 specimens), **MacGillivray Reef** (2 specimens), **Ribbon Reef, Hope Island** (4 specimens), **Low Isles, Palm Islands** (29 specimens), **Pandora Reef** (13 specimens); **Magnetic Island** (5 specimens), **Bowling Green Bay, Bait Reef, Whitsunday Islands** (9 specimens), **Swain Reefs, Masthead Reef, Wistari Reef** (4 specimens).

These localities include collecting stations 18, 26, 27, 28, 34, 36, 37, 38, 41, 42, 43, 45, 57, 59, 60, 65, 74, 79, 90, 92, 97, 102, 111, 117, 119, 120, 122, 125, 126, 129, 130, 131, 132, 133, 135, 137, 138.

Previous records from Eastern Australia

Port Denison (as *T. speciosa*) Bernard (1896); **Great Barrier Reef** (as *T. mesenterina, T. venusta, ?T. crassa*) Bernard (1896).

Characters

Colonies are composed of unifacial laminae which are oriented in a more vertical than horizontal plane. These laminae may be flat or regularly curved or irregularly folded. The degree of folding varies greatly (see below), with upper margins fusing to form tubes with the corallites either on the inside or outside. In extreme development, colonies consist of a dense mass of folds and tubes. Corallites are small (2.5-3.5 mm diameter), either tubular or conical, usually protuberant and strongly inclined towards a vertical orientation. Older corallites become increasingly deeply embedded in coenosteum, those on concave surfaces, especially towards the base of coralla, frequently becoming submerged. Otherwise, the appearance of corallites is relatively uniform within the same corallum. Calices are circular, 1.3-2 mm diameter. Three orders of septa can often be distinguished, the first two equal or subequal, the third abortive. The major septa extend inwards $\frac{1}{3}$-$\frac{2}{3}$ the septal radius, then plunge steeply into the fossa, which is usually deep. They remain visibly separated from the columella. All septa are usually heavily granulated. In larger corallites of some coralla there may be some fusion of septa along their inner margins. The development of the columellae varies greatly. They are usually elliptical, spongy, and very protuberant. In some corallites, they may be reduced to a simple vertical ridge or plate. The coenosteum is usually very porous.

Colonies are mostly uniform in colour, pale grey-green or grey-brown being the most common colour in most biotopes. Polyps are usually white.

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2 A specimen labelled 'type' in the University of Glasgow appears to be Bernard's specimen, not Ellis & Solander's.

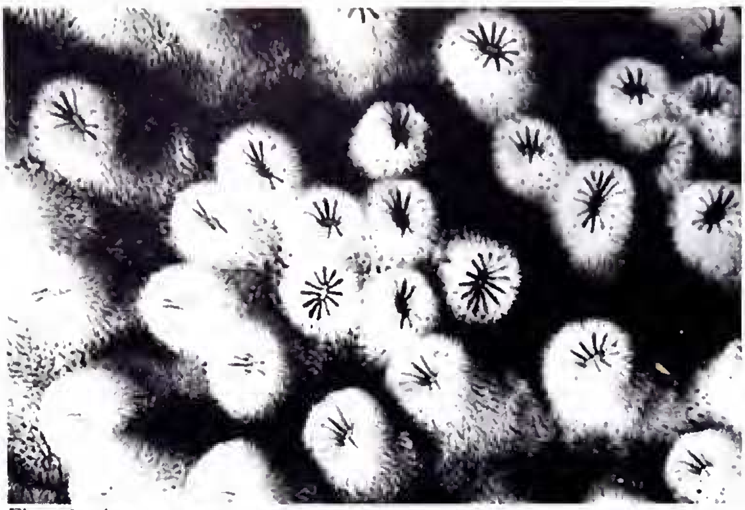


Fig. 686 ▲

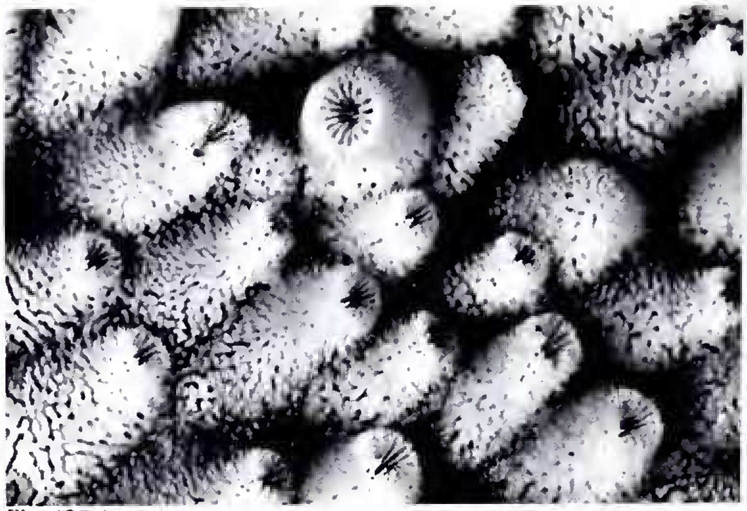


Fig. 687 ▲

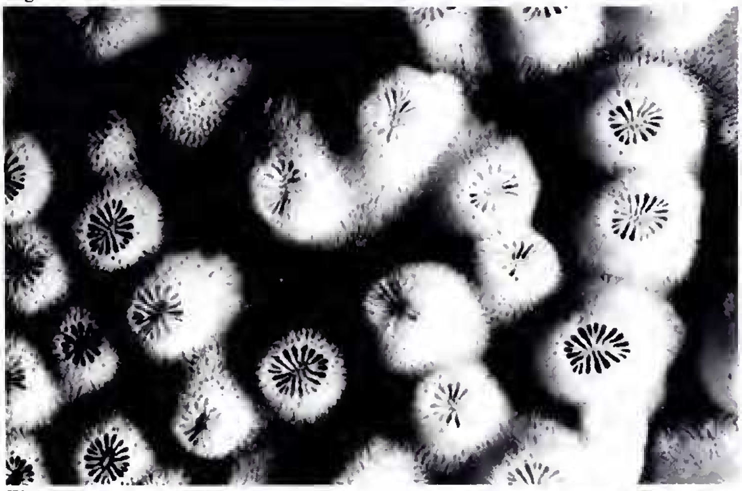


Fig. 688 ▲

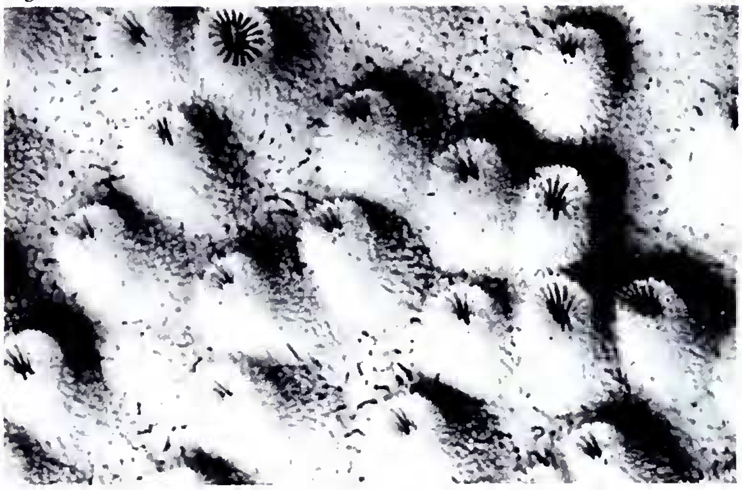


Fig. 689 ▲

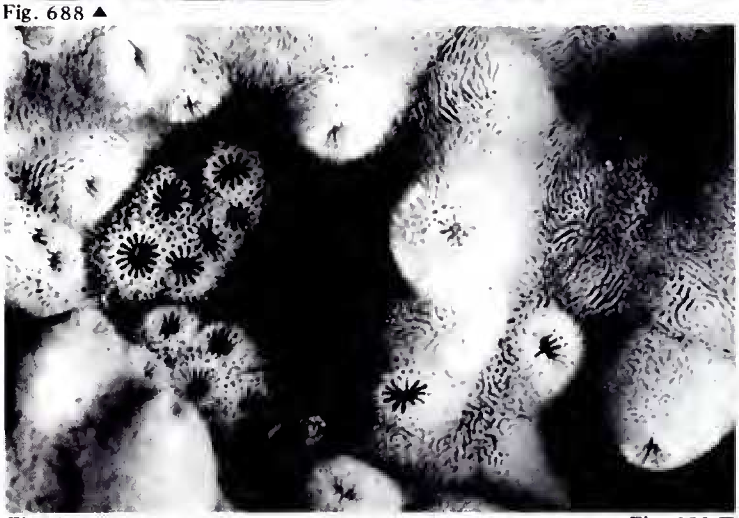


Fig. 690 ▲

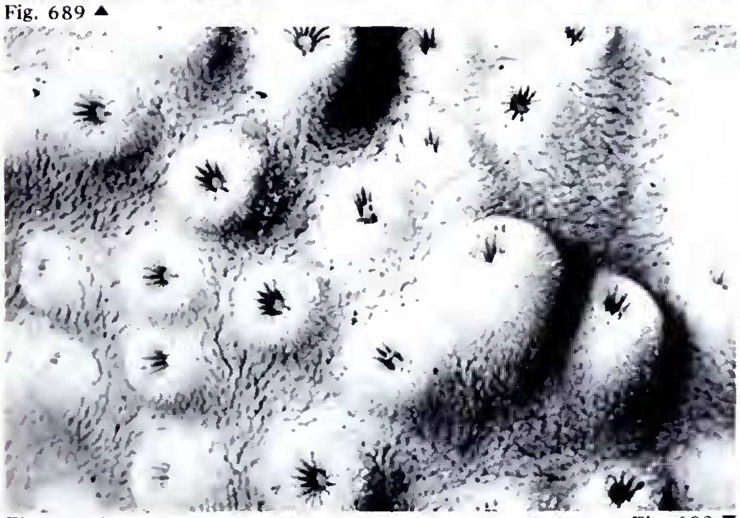


Fig. 691 ▲

Fig. 692 ▼

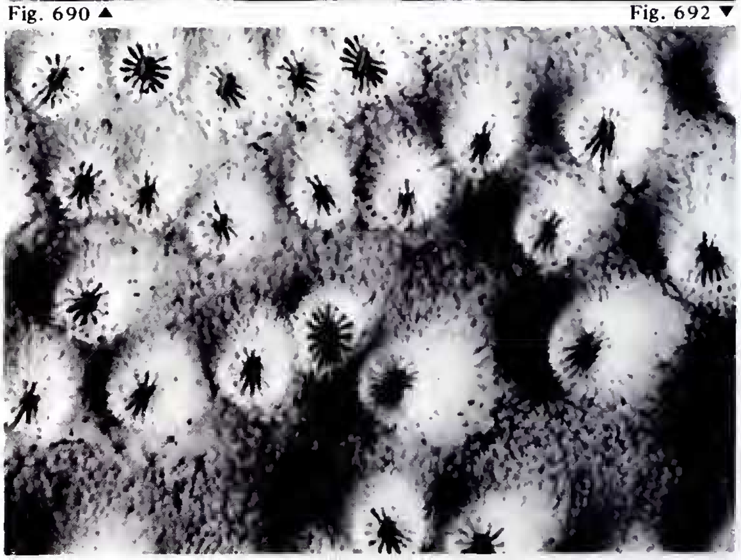
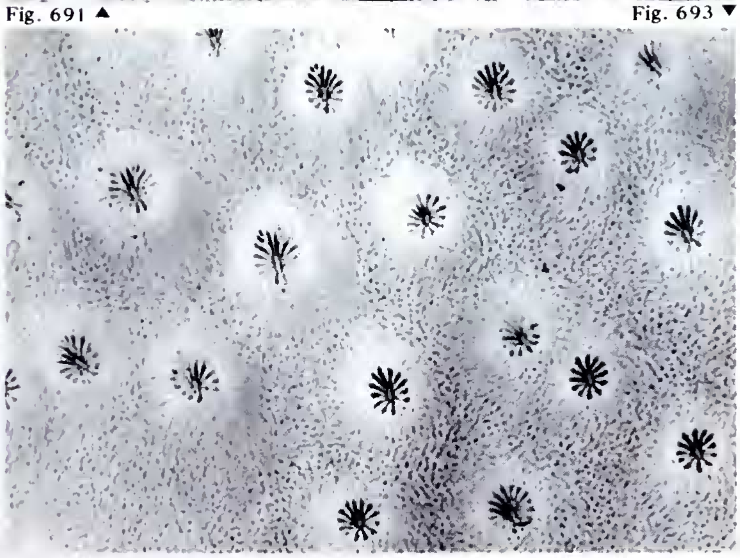


Fig. 693 ▼



Skeletal variation

This very common species has a very wide growth form variation, most of which normally occurs in the first 10 m of its bathymetric range (Figs. 680, 681, 683-685). On steeply sloping substrates, individual large colonies may show much of this variation.

Turbinaria mesenterina from intertidal biotopes.

Colonies frequently form 'microatolls' with dead centres and growing perimeters composed of tightly convoluted fronds which frequently form irregular, anastomosing tubes. Corallites are relatively large, closely packed, thick walled and conical in shape. Mature calices average approximately 1.7 mm diameter. Septa are well developed and occupy most of the calicular fossa. The columellae are usually small.

Turbinaria mesenterina from shallow biotopes.

Colonies show a very wide range of growth form which is closely related to water depth. At the upper limit, colonies have similar growth forms to those from intertidal biotopes, at the lower limit their fronds lose their tight convolution and become flattened or wavy. Mature corallites are usually more tubular than conical and usually project up to 3 mm from the lamina. They have the full range of calicular characters described above.

Turbinaria mesenterina from biotopes with reduced light intensity.

Colonies growing in relatively deep water (>10 m in most biotopes but 20 m in very clear water) usually lose any sign of having convoluted fronds. Rather, fronds become flat, with an irregular orientation or form regular whorls (Fig. 845). Corallites are fine and tubular and usually a little protuberant. Septa are very fine and frequently of irregular length, some having fused inner margins. In extreme development, colonies consist of fine, nearly horizontal laminae, with tiny, widely spaced corallites embedded in the coenosteum.

Affinities

Turbinaria mesenterina is closest to *T. reniformis* and the two species (Figs. 843, 844) may sometimes be difficult to distinguish in heterogeneous collections. As noted below (p. 395) *T. mesenterina* is usually more convoluted than *T. reniformis*, has thinner, more tubular corallites and usually a third (alternating) order of septa, whereas the septa of *T. reniformis* are equal or subequal.

Distribution

Widely distributed throughout the tropical Indo-Pacific from the Red Sea and east African coast to the western Pacific including the Marshall Islands and Fiji.

Turbinaria reniformis Bernard, 1896

Synonymy

Turbinaria reniformis Bernard, 1896.

?*Turbinaria reptans* Bernard, 1896.

Figs. 686-693 *Turbinaria mesenterina* (× 0.5).

Figs. 686, 690, 693	From Geoffrey Bay, Figs. 686, 690, same coralla as Figs. 679, 682 respectively.
Figs. 687, 689, 691, 692	From Pandora Reef; Figs. 689, 691, 692, same coralla as Figs. 681, 683, 684 respectively.
Fig. 688	From Happy Bay, Long Island, Whitsunday Islands, collecting station 102.

?*Turbinaria lichenoides* Bernard, 1896.

?*Turbinaria veluta* Bernard, 1896.

Turbinaria sp. cf. *T. veluta* (Bernard); Wells (1954); Scheer & Pillai (1974).

Turbinaria reniformis, T. reptans and *T. lichenoides* all have their type localities within the Great Barrier Reef. The holotypes of the latter two nominal species are very similar to each other and appear to be very shallow water growth forms of *T. reniformis.*

This species, which is one of the most common eastern Australian *Turbinaria*, appears to be the same as the *T.* sp. cf. *veluta* from the Marshall Islands described by Wells (1954) who wrote, 'this form, which may represent a new species . . . seems to be linked to *T. veluta* by the peculiar coenenchyme, as described by Bernard . . .'. Wells' figures of this species are very close to part of the range of the present species and his descriptions of living colonies also closely agree. Likewise, the *T.* sp. cf. *veluta* of Scheer & Pillai is probably the same species. However, Bernard's type of *T. veluta* cannot conclusively be associated with this species, hence another name is selected for it.

Material studied

Big Mary Reef (2 specimens), **Yorke Island** (2 specimens), **Murray Islands** (6 specimens), **Newman Reef** (4 specimens), **Ribbon Reefs** (5 specimens), **Jewell Reef, Bewick Island, Lizard Island** (4 specimens), **Low Isles** (2 specimens), **Palm Islands** (25 specimens), **Pandora Reef** (8 specimens), **Magnetic Island** (2 specimens), **Whitsunday Islands** (8 specimens), **Pompey Complex, Swain Reefs** (2 specimens).

These localities include collecting stations 1, 2, 4, 5, 9, 11, 14, 17, 20, 57, 60, 88, 90, 136, 149, 150, 154, 156, 167, 169, 170, 175, 176, 177, 228, 229.

Previous records from Eastern Australia

? **Torres Strait** (as *T. reptans*) Bernard (1896); **Palm Islands**, Bernard (1896); **Townsville** (as *T. lichenoides*) Bernard (1896).

Characters

This species is widespread and abundant and shows a wide range of growth form, sometimes within the one colony. This range is similar to that of *T. mesenterina* which frequently cohabits similar biotopes (Figs. 843, 844). Colonies are composed of unifacial laminae which may be encrusting, flat, regularly curved or irregularly folded. Large colonies (up to 5 m diameter) are frequently composed of tiers of plates, those near the bottom being regular in shape, horizontal and up to approximately 40 cm across, those near the top being sub-vertical and folded.

The structure and appearance of the corallites varies greatly. In some coralla or parts of coralla they are crowded close together so that they are almost in contact. Usually, centres are separated by areas of flat, smooth coenosteum. They are almost always conical in shape with thick thecae and small calices. Septa are initially in two complete, equal or subequal cycles. The majority of coralla in a large collection from the Palm Islands retain 12 septa in almost all mature corallites. However, coralla from other localities may have an average of up to 20 septa in mature corallites. These are usually equal although there may be fusion of the inner margins of groups of 2 or 3 septa in some corallites. Septa are characteristically wedge shaped with fine, vertical, straight or slightly dentate inner margins and expanded peripheral margins where

Figs. 694-696 *Turbinaria reniformis* (× 0.5).

Figs. 694, 695 From Nara Inlet, Hook Island, Whitsunday Islands, collecting station 97.
Fig. 696 From the Swain Reefs, collecting station 69.

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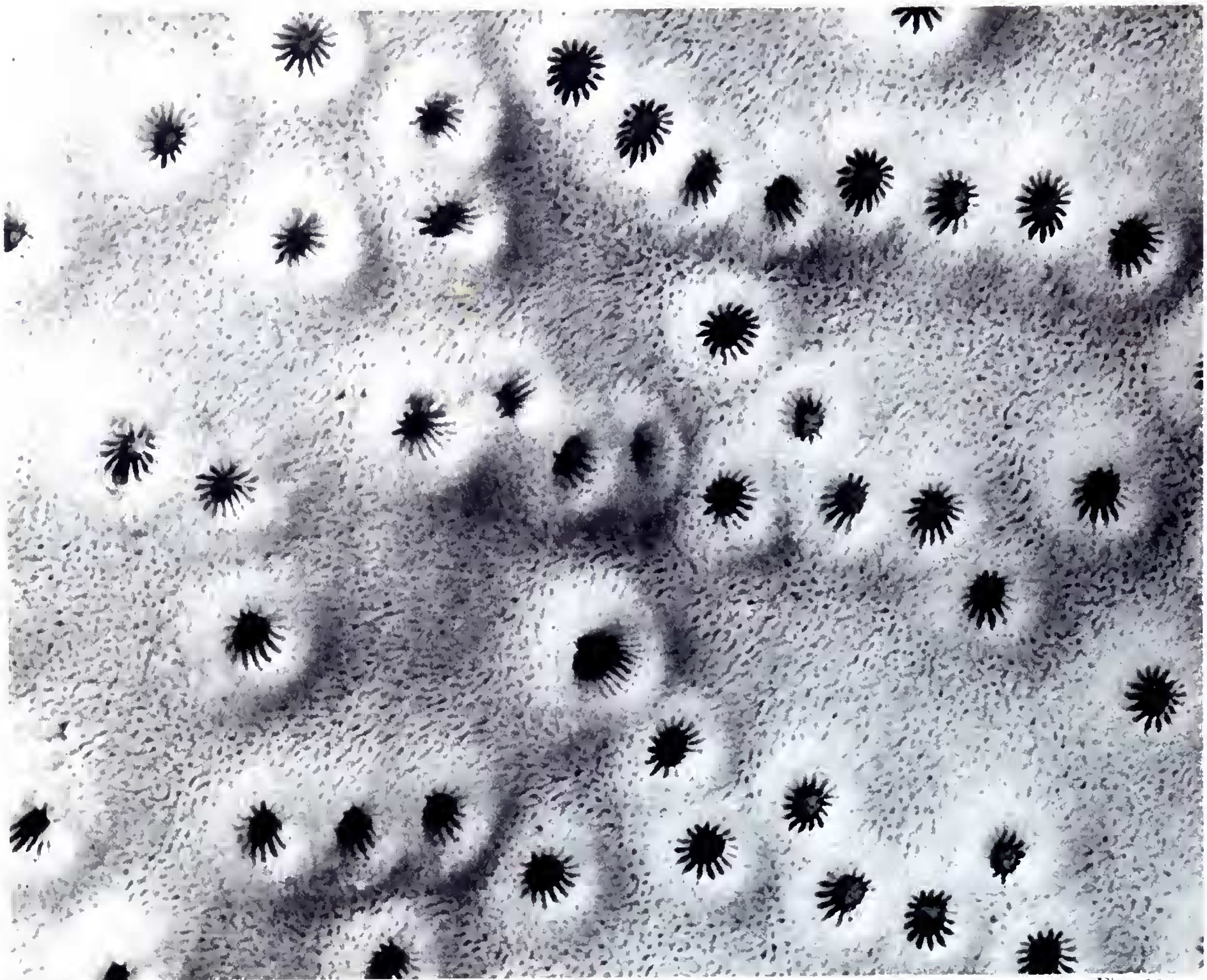
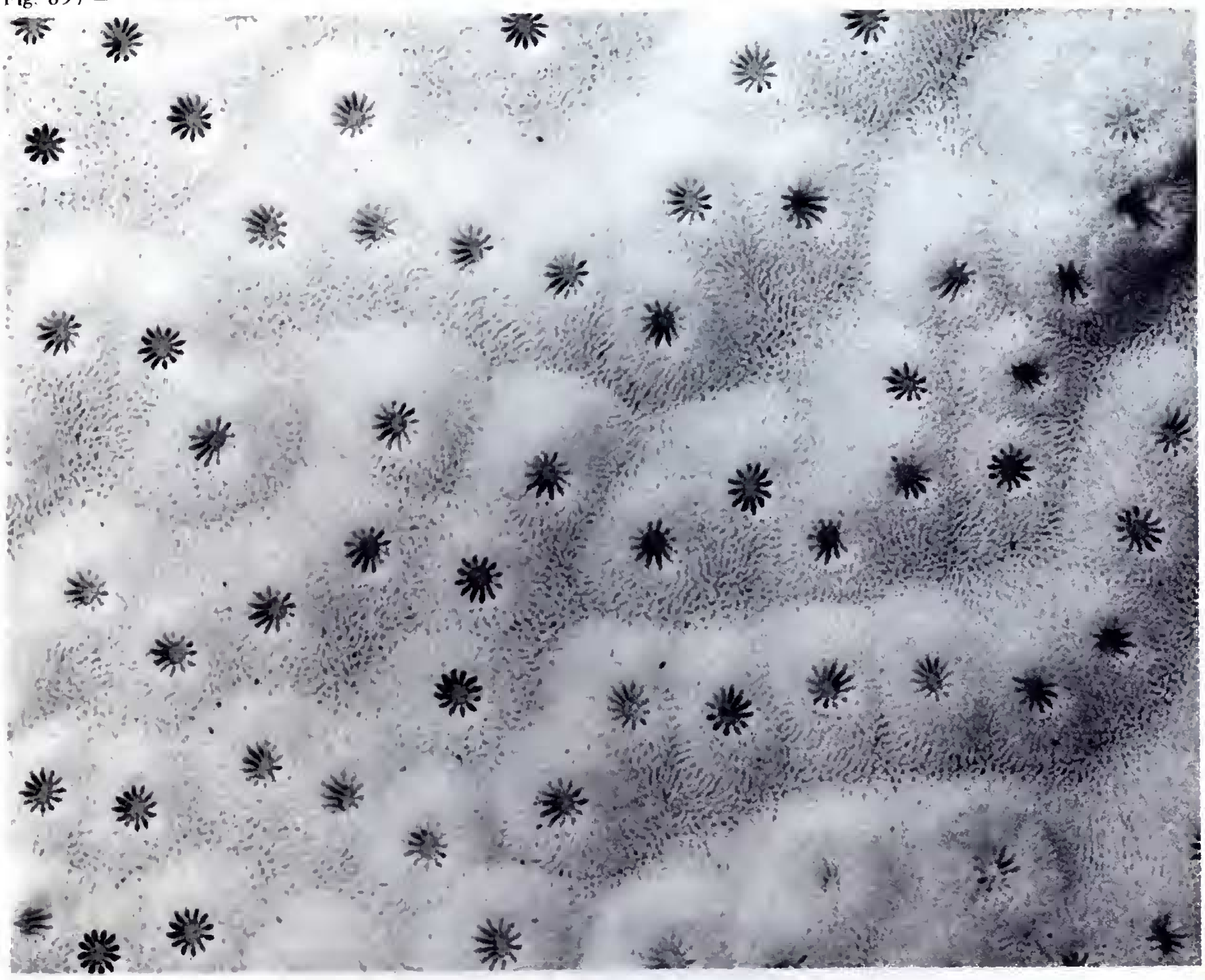


Fig. 697 ▲

Fig. 698 ▼



synapticular rods of adjacent septa converge towards each other in the matrix of the theca. All septa are heavily granulated. The appearance of the columellae varies greatly from a thin, vertical plate to a spongy dome, the latter being more prevalent in corallites with relatively open calices.

Colonies are usually yellow-green around the margins of plates with darker older areas. Polyps are usually yellow.

Skeletal variation

As with *T. mesenterina* this species has a wide range of growth forms which are closely correlated with depth over the first 10 m of its bathymetric range. However, colonies in the same biotope and at the same depth may have different growth forms. Clearly, this is related to differences in exposure to light but also appears to be related to age, young colonies or parts of colonies having brighter colours and smaller, more protuberant corallites. Such corallites usually have small, deep calices, with elongate or even plate-like columellae. With subsequent growth the calice diameter usually increases and the columellae become larger and rounder. Older calices, however, become increasingly submerged in coenosteum.

Affinities

This species is usually readily recognised underwater (see Figs. 694-698) but in heterogeneous collections may be difficult to distinguish from others, especially *T. mesenterina*, which is also very variable. The latter has thinner, more tubular corallites and frequently has a third (alternating) septal cycle. The growth form of both species overlaps to some degree, although *T. reniformis* seldom becomes as convoluted as *T. mesenterina*. Encrusting or sub-glomerate growth forms are also easily confused with *T. stellulata* (see p. 400).

Distribution

The few previous records of this species are from the Nicobar Islands, the Marshall Islands, Tonga and the Cook Islands.

Turbinaria stellulata (Lamarck, 1816)

Synonymy

Astraea stellulata Lamarck, 1816.

Astreopora stellulata (Lamarck); de Blainville (1834); Dana (1848).

Turbinaria stellulata (Lamarck); Quelch (1886); Bernard (1896); Yabe & Sugiyama (1941); Wells (1954); Ma (1959).

Turbinaria globularis Bernard, 1896.

Turbinaria subversa (Bernard), 1896.

?*Turbinaria elegans* Bernard, 1896; *non* Yabe & Sugiyama (1941); *non* Ma (1959).

Turbinaria sp. nov.? Yabe & Sugiyama, 1941 (Pl. C., Fig. 4 only).

Turbinaria stephensoni Crossland, 1952; Nemenzo (1962).

?*Turbinaria mantonae* Crossland, 1952.

The holotype of *T. stellulata* is a small piece of a thick, encrusting colony. Corallites are mostly non-protuberant although larger ones have a slightly raised rim. They are separated 2-5 mm. The septa are short, with well developed columellae occupying up to half the corallite diameter. The columellae are spongy and frequently have an axial plate. Most of Bernard's *T. stellulata* differ from the type in having more

Figs. 697, 698 *Turbinaria reniformis* (× 2.5).

Fig. 697 From Nara Inlet, Hook Island, same corallum as Fig. 694.
Fig. 698 From the Swain Reefs, same corallum as Fig. 696.

protuberant corallites (as have most specimens of the present series) and Crossland (1952) appropriately noted that 'Bernard p. 65 refers the species *T. stellulata* to Blainville and Lamarck, but on very slender grounds'.

Bernard (1896) divided his 'turbinariae glomeratae' into four species, *T. stellulata, T. palifera, T. parvistella* and *T. globularis*, the last a new species. Of *T. stellulata* and *T. globularis*, Bernard wrote 'no two of these specimens are alike, and they could and perhaps should be arranged under eight different headings. I have, however, divided them into two groups under the name *stellulata* and *globularis*, accordingly as the calices are generally immersed and protuberant.' One of Bernard's two *T. globularis* is from the Palm Islands where *T. stellulata* is common. The type specimen, from Diego Garcia, has more protuberant corallites with acute margins.

One of Bernard's *T. stellulata* comes very close to one of his *T. elegans* from the Great Barrier Reef, the main difference being in growth form which is plate-like in the latter species. The holotype of *T. elegans* has slightly protuberant corallites, but is not clearly associated with the present species.

Turbinaria parvistella Saville-Kent, 1871 was accepted as a valid species by Bernard but this study supports Crossland's (1956) view that it cannot be identified from the description. The type specimen appears to be lost.

According to Crossland, his two specimens of *T. stephensoni* differ from his *T. stellulata* in having 'most of the long septa very clearly joining the columella, and sometimes bearing a knob just before they join' as well as having a columella which is 'very distinctive'. Crossland's specimens are clearly the same as most of the specimens of the present series. *Turbinaria mantonae* appears to belong to the same species although the calicular structures of the type specimens are very different. Syntype 1934.5.14.430 of *T. mantonae* is submassive with slightly protuberant corallites. Calices are deep and septa have very well defined, vertical, non-anastomosing inner margins, in marked contrast to the sloping, anastomosing septa of *T. stephensoni.* The present series, however, contains a full range of intermediate forms and most of the range of corallite structure can sometimes be found in the one corallum. In the latter case, *mantonae*-like corallites are normally found on submassive parts of coralla, while *stephensoni*-like corallites usually occur towards the corallum periphery.

Material studied

Anchor Cay (3 specimens), **Campbell Islet** (3 specimens), **Big Mary Reef, Yorke Island** (3 specimens), **Warrior Reef, Murray Island** (10 specimens), **Dungeness Reef, Newman Reef** (5 specimens), **Houghton Island, Lizard Island** (7 specimens), **Eyrie Reef** (2 specimens), **Ribbon Reef** (4 specimens), **Plug Reef, Palm Islands** (7 specimens), **Pandora Reef** (5 specimens), **Whitsunday Island** (3 specimens), **Pompey Complex, Frigate Cay, Swain Reefs, Masthead Island**.

These localities include collecting stations 11, 19, 26, 27, 28, 36, 40, 41, 43, 49, 57, 63, 64, 69, 81, 97, 99, 100, 102, 103, 111, 121, 122, 125, 129, 131, 132, 135, 139.

Previous records from Eastern Australia

Lizard Island (as *T. mantonae*) Crossland (1952); **Low Isles** (as *T. stephensoni*) Crossland (1952); **Palm Island** (as *T. globularis* and *T. subversa*) Bernard (1896).

Figs. 699-701 *Turbinaria stellulata* (× 0.7).

Fig. 699 From the Swain Reefs, collecting station 69.
Fig. 700 From Lizard Island, collecting station 100.
Fig. 701 From Ribbon Reef, collecting station 65.

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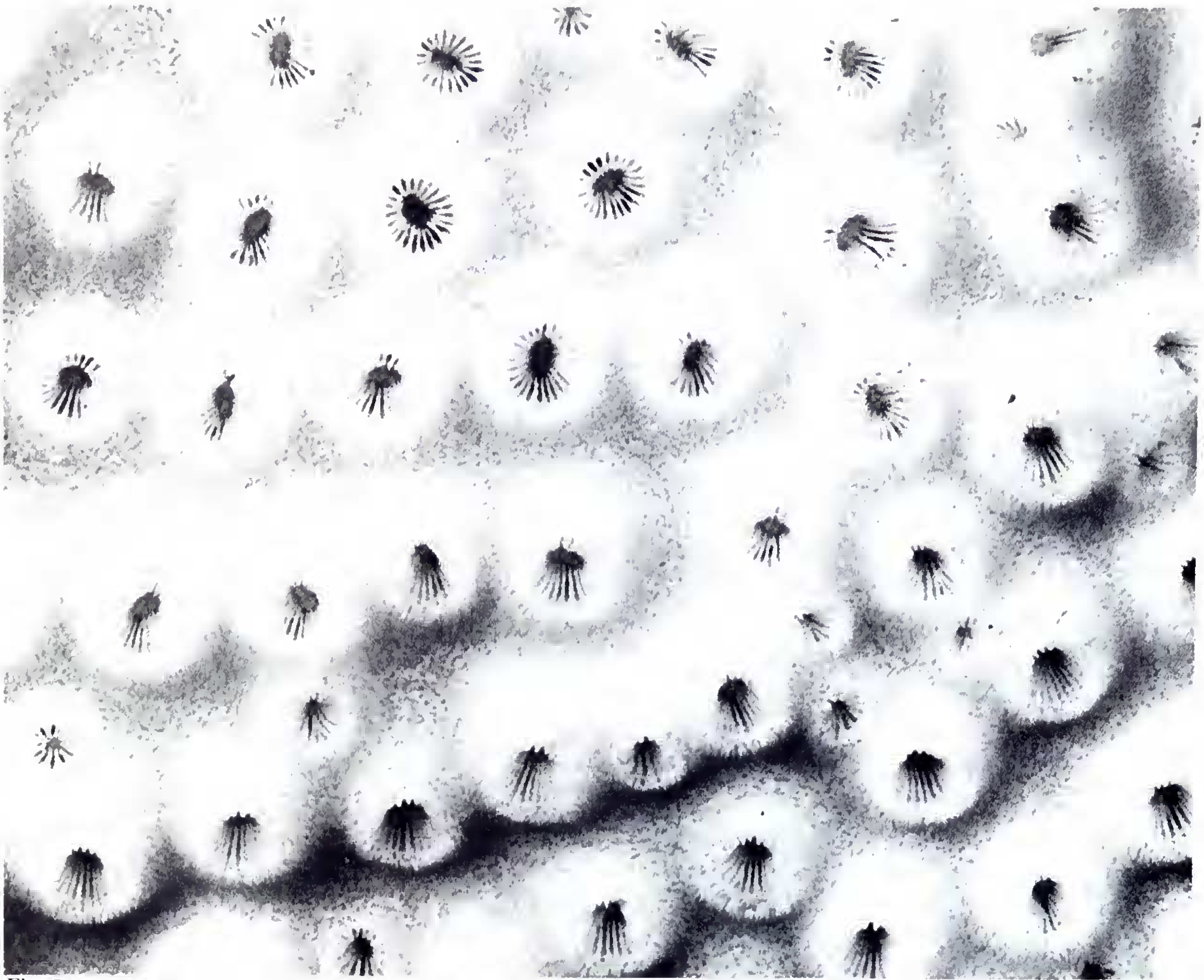
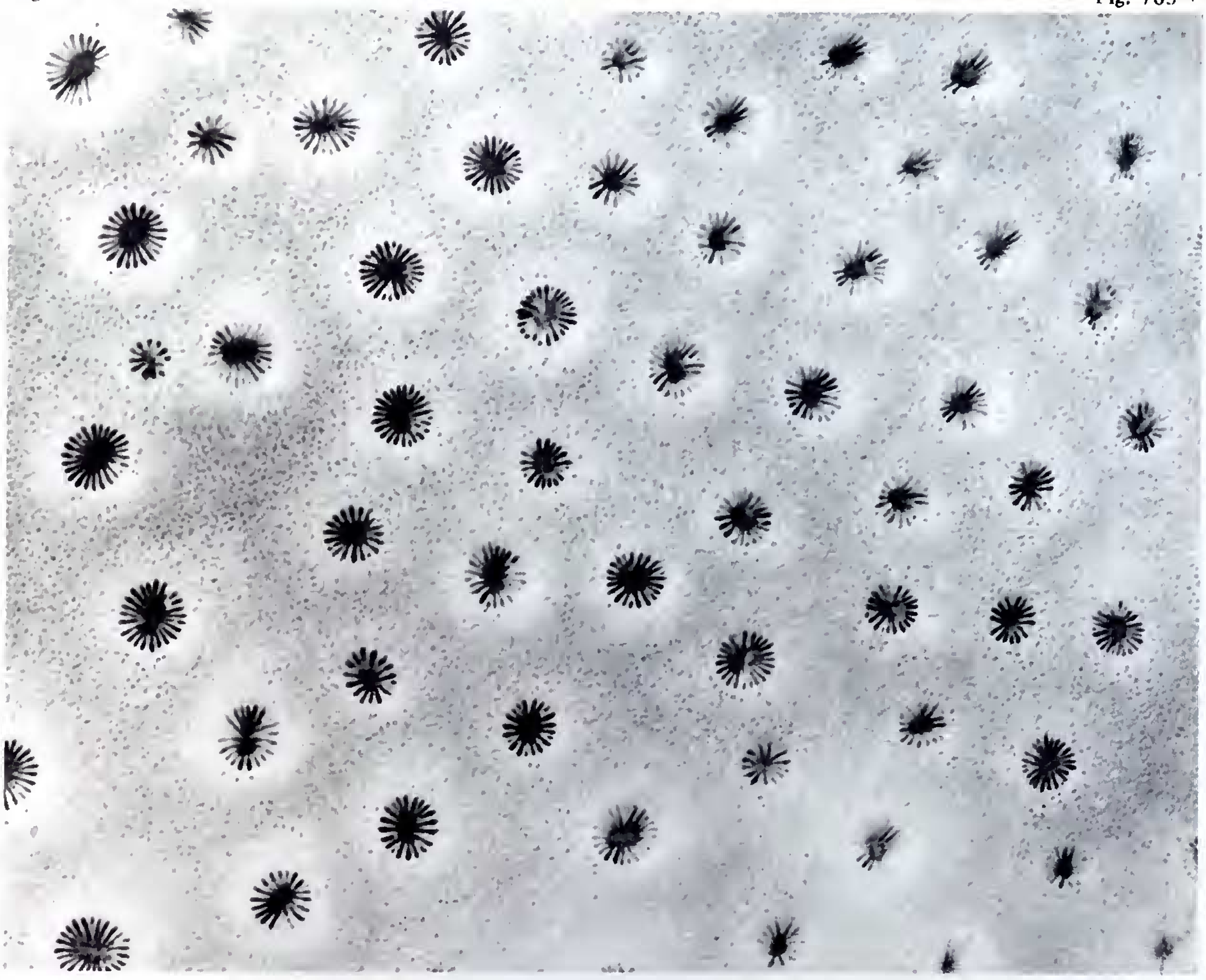


Fig. 702 ▲

Fig. 703 ▼


Characters

Coralla form massive dome-like colonies by repeated overgrowths of plate-like or subspherical expansions (Fig. 705, 851, 852). Small coralla consist only of plates which usually grow close to the substrate (Fig. 853). Mature corallities have well defined thecae. They are conical in shape and normally protrude up to 2 cm from the lamina and are 3-4 mm diameter. Calices are wide (approximately 2 mm) giving the corallites an open appearance. Septa slope from the rim to the columellae; sometimes they have vertical inner margins. As noted by Crossland (for *T. stephensoni*) the septa may be of irregular length and short septa may curve towards longer ones and have their inner margins anastomosed. All septa are covered with granules or fine spinules and have finely dentate inner margins. The columellae are circular to elliptical and may be very thin and elongate. There is usually a tuberculated ridge down the axis which, in some coralla, is very prominent. The coenosteum is spongy, without distinctive ornamentation. The undersurfaces of plates usually have a well defined edge zone, a narrow band of epitheca and an inner area overgrown by encrusting organisms.

Living colonies have a wide variety of colours with brown and green predominating.

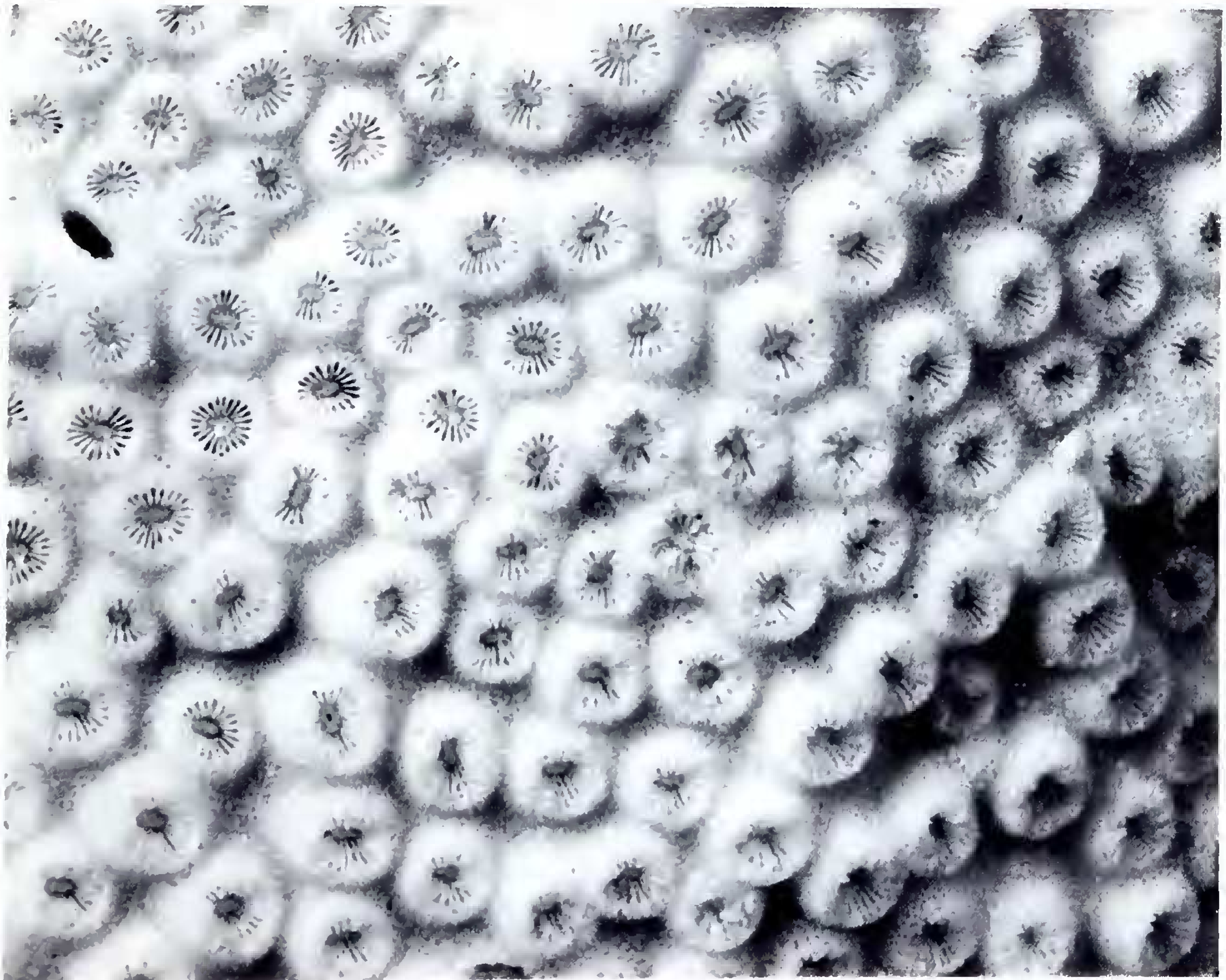
Affinities

As noted above (p. 374), the present collections contain specimens which are close to *T. stellulata* but which cannot be reliably included in it. This is largely because

Figs. 702-704 *Turbinaria stellulata* (× 2.5).

Fig. 702 From Ribbon Reef, same corallum as Fig. 701.
Fig. 703 From Lizard Island, same corallum as Fig. 700.
Fig. 704 From the Swain Reefs, same corallum as Fig. 699.

Fig. 704 ▼



the species shows substantial geographic as well as environmentally induced variation and coralla from one region usually show greater similarity with each other than with coralla from similar biotopes of other regions. However, the present study has not revealed the presence of more than one characteristically glomerate species of *Turbinaria* in any one biotope and there is no clear evidence to suggest that more than one such species is present on the Great Barrier Reef. Further study may demonstrate the presence of geographically restricted subspecies, or may reveal additional rare, or geographically restricted, species.

Sub-glomerate colonies of *T. reniformis* may closely resemble *T. stellulata in situ* (Fig. 854) but are usually distinguished underwater by comparison with nearby foliaceous colonies (if present). Sub-glomerate coralla from the same or similar biotopes are readily separated by *T. reniformis* having thicker walled, conical corallites, with broad bases but relatively narrow apertures. Sub-glomerate *T. reniformis* are less easily distinguished in heterogeneous collections as both species show wide variation in calicular structures. However, differences in corallite shape usually apply and *T. reniformis* usually has septa (usually 12) of equal length, with straight margins.

Most *T. reniformis* are distinguished by growth form alone and *T. stellulata* does not closely resemble any other east Australian *Turbinaria* except *T. radicalis*, which has an encrusting growth form but is readily distinguished by the presence of rootlets and also by its smaller, usually less protuberant corallites.

Distribution

Present records indicate a distribution west to the South China Sea, east to the Marshall Islands and south to the Great Barrier Reef and Fiji.

Turbinaria bifrons Brüggemann, 1877

Synonymy

Turbinaria bifrons Brüggemann, 1877a; Rehberg (1892); Bernard (1896); Matthai (1923a); Yabe & Sugiyama (1941); Crossland (1952); Utinomi (1965, 1971).

Fig. 705 *Turbinaria stellulata* from Ribbon Reef, same colony as Figs. 701, 702.

Turbinaria aequalis Quelch, 1886.

Turbinaria dendrophyllia Bernard, 1896; Ma (1959).

? *Turbinaria conspicua* Bernard, 1896.

Turbinaria gracilis Bernard, 1896.

? *Turbinaria nidifera* Bernard, 1896.

The four species of Bernard make up his 'Turbinariae Bifrontales': 'Turbinarians in which the margin of the cup forms vertical folds, which fuse back to back; the subsequent growth of the stock is carried on by these folds, which thus form fronds with calices on both sides.' Bernard recorded all these species from Australia, the latter two from the Great Barrier Reef. He himself commented that *T. conspicua* is very close to *T. bifrons* and that *T. gracilis* shows only a minor variation from *T. conspicua*. *Turbinaria dendrophyllia* is known from two specimens from Roebuck Bay, Western Australia, which are only provisionally grouped together. All these species, however, appear to fall within the range of the present series, which is clearly one, distinct, species.

Turbinaria aequalis Quelch is included in the present species on the basis of the original description; the holotype has not been re-examined.

Material studied

Bramble Cay, Campbell Island (2 specimens), **Warrior Reef** (11 specimens), **Jervis Reef** (5 specimens), **Thursday Island, Palm Islands** (8 specimens), **Magnetic Island** (12 specimens), **Wistari Reef** (3 specimens), **Heron Island** (3 specimens).

These localities include collecting stations 42, 53, 59, 60, 116, 117, 119, 120, 121, 128, 132.

Previous records from Eastern Australia

Wednesday Island (as *T. aequalis*) Quelch (1886); **Thursday Island** (as *T. conspicua*) Bernard (1896); **Low Isles**, Crossland (1952); **Port Molle** (as *T. conspicua*) Bernard (1896); **Great Barrier Reef** (as *T. gracilis* and *T. nidifera*) Bernard (1896).

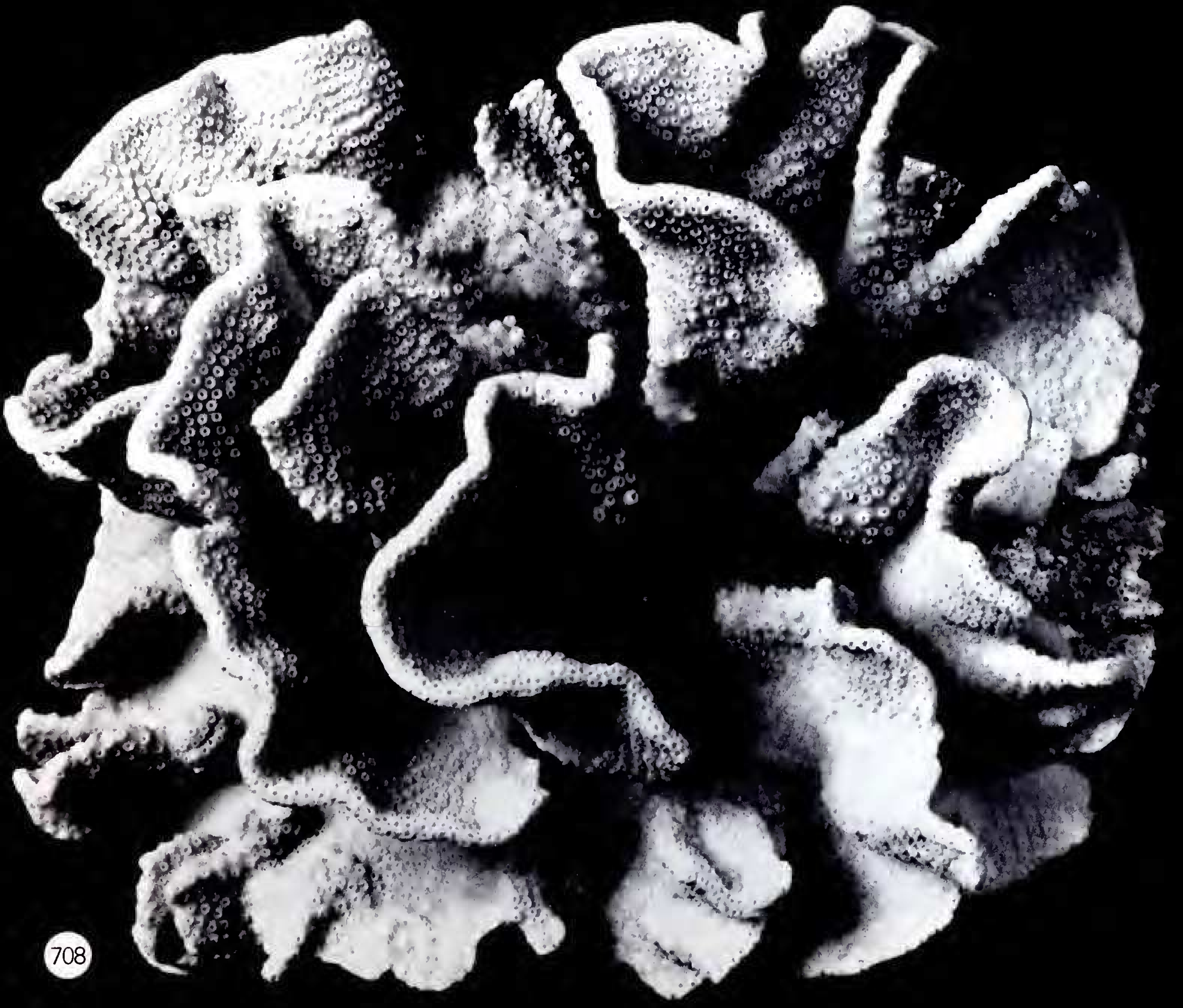
Characters

Small colonies are approximately cup-shaped with irregular, wavy margins and folded surfaces, the folds radiating from the colony centre (Figs. 706, 855). The undersurface of such colonies is smooth and free of corallites, the whole colony being raised on a stalk, usually with a broad holdfast. Larger colonies may retain the original cup shape or may become completely irregular depending mainly on available space for growth. The upward folds may develop into tall, straight or wavy, near vertical fronds which may remain connected to the marginal fold or may become isolated from the margin. In the latter case the fronds may remain thin (almost columnar), may occasionally become tubular, may divide into sub-fronds or may become interconnected. The latter process can become strongly developed, colonies becoming a mass of wavy, interconnected fronds with irregular margins. In all cases fronds are bifacial with equal corallite development on each side. They are normally <1 cm thick near the margins and do not show substantial secondary thickening except near their bases.

The appearance and structure of the corallites varies according to their position on the corallum. Those at the corallum centre are usually small (<2 mm diameter) and become submerged in the coenosteum. On the fronds they are usually strongly inclined towards the margins with the outward facing (distal) part of the thecae emerged 2-6 mm. Corallites at the corallum centre tend to be conical; those on the fronds tubular, with round or elliptical openings. Budding occurs at the frond margins on either side of a central plate or pair of plates. Corallites are usually evenly


707


706


708

spaced and have a regular appearance. The number of septa varies from 12 to 22 in different coralla but are relatively uniform in number within the same corallum. They are of the same order and some may be anastomosed. They extend inward $\frac{1}{2}$ to $\frac{3}{4}$ the calice radius and have straight or inwardly curved margins. They are very granulated and thus occupy much of the central space of the calices. The columellae have a marked plate-like, directive ridge, usually perpendicular to the frond surface. They usually lie deep within the calices with the septa adjoined to their upper edges.

Living colonies do not have distinctive colours. They are usually a uniform grey, green or brown, usually with darker calices. This species is relatively uncommon, and is usually found in partially protected biotopes among other *Turbinaria* species.

Affinities

As this is the only Eastern Australian species which forms narrow, bifacial fronds, large colonies are very readily recognised. Other species of *Turbinaria* may have folds coming into contact back-to-back, but this occurs irregularly and the folds subsequently separate. Small coralla of *T. bifrons* are much less easily recognised, especially if bifacial fronds are not developed. In such case they may be particularly difficult to distinguish from *T. frondens*. Calices are more regular and slightly smaller than those of *T. frondens*, septa may anastomose and usually reach the collumellae near their tops rather than their bases as in *T. frondens*. However, coralla of these species from different biotopes cannot be reliably separated on the basis of calicular structures alone.

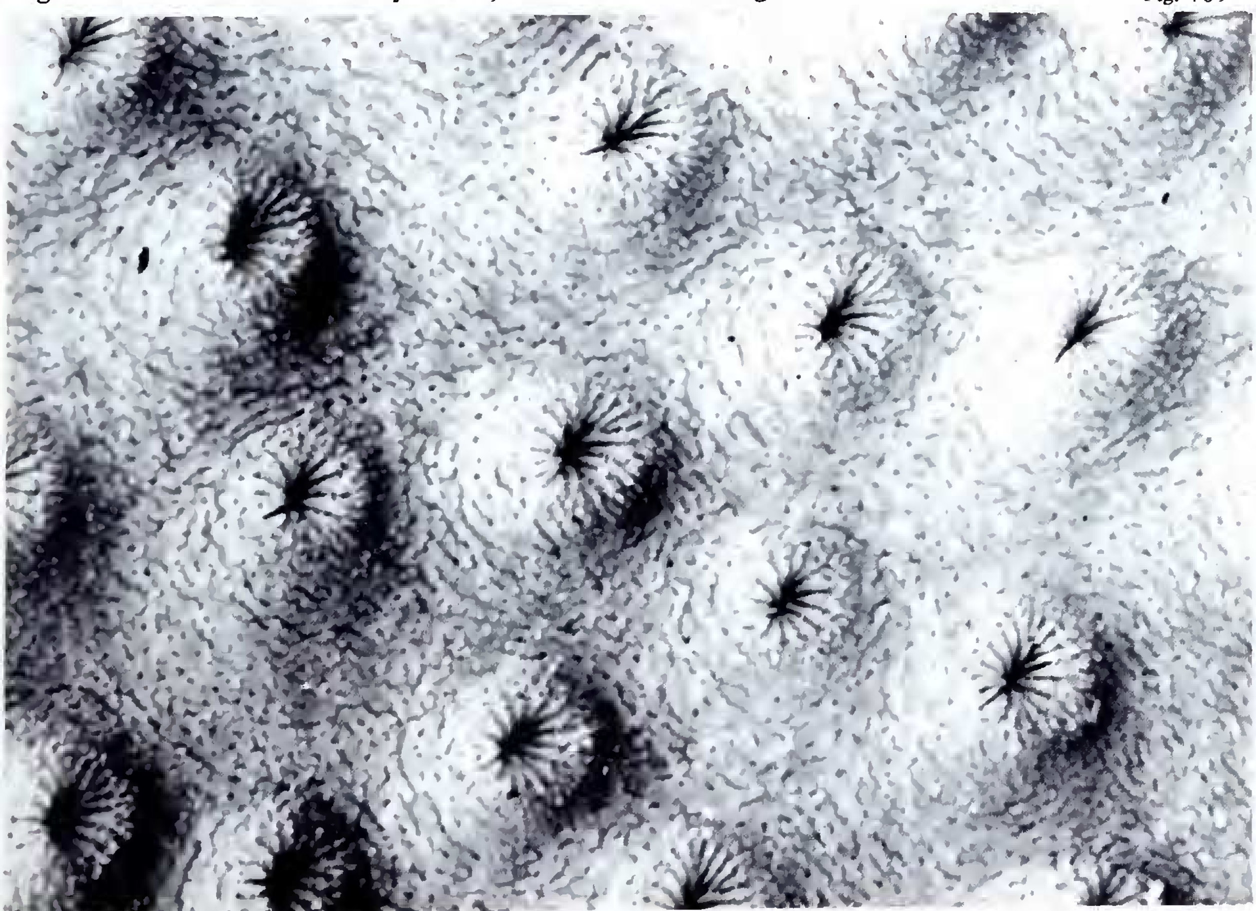
Figs. 706-708 *Turbinaria bifrons.*

Fig. 706 From Thursday Island, collecting station 53 (× 0.33).
Fig. 707 From Warrior Reef, collecting station 120 (× 0.33).
Fig. 708 From Big Mary Reef (× 0.7).

Figs. 709-711 *Turbinaria bifrons* (× 10.0).

Figs. 709, 710 From Magnetic Island.
Fig. 711 From Thursday Island, same corallum as Fig. 706.

Fig. 709 ▼



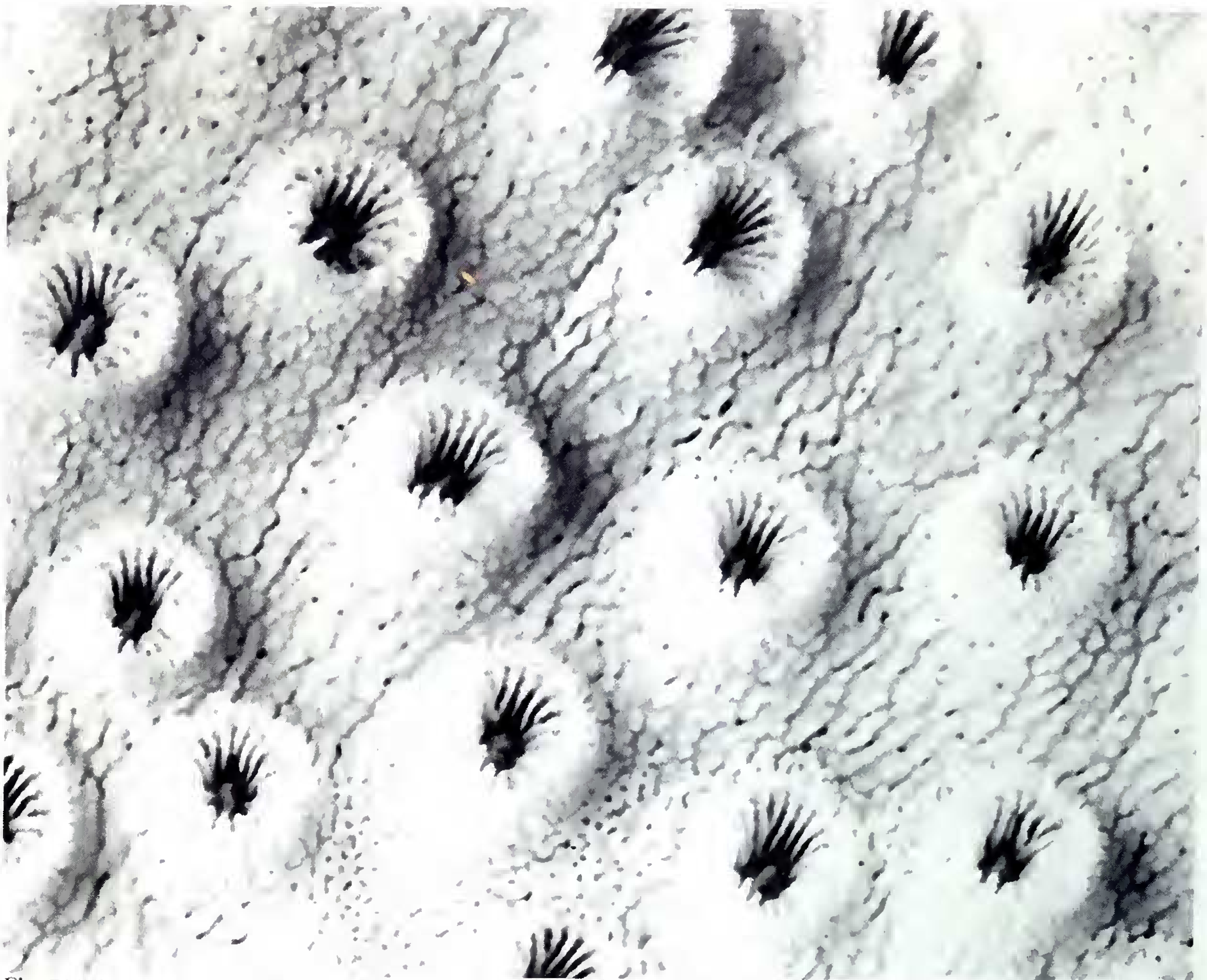
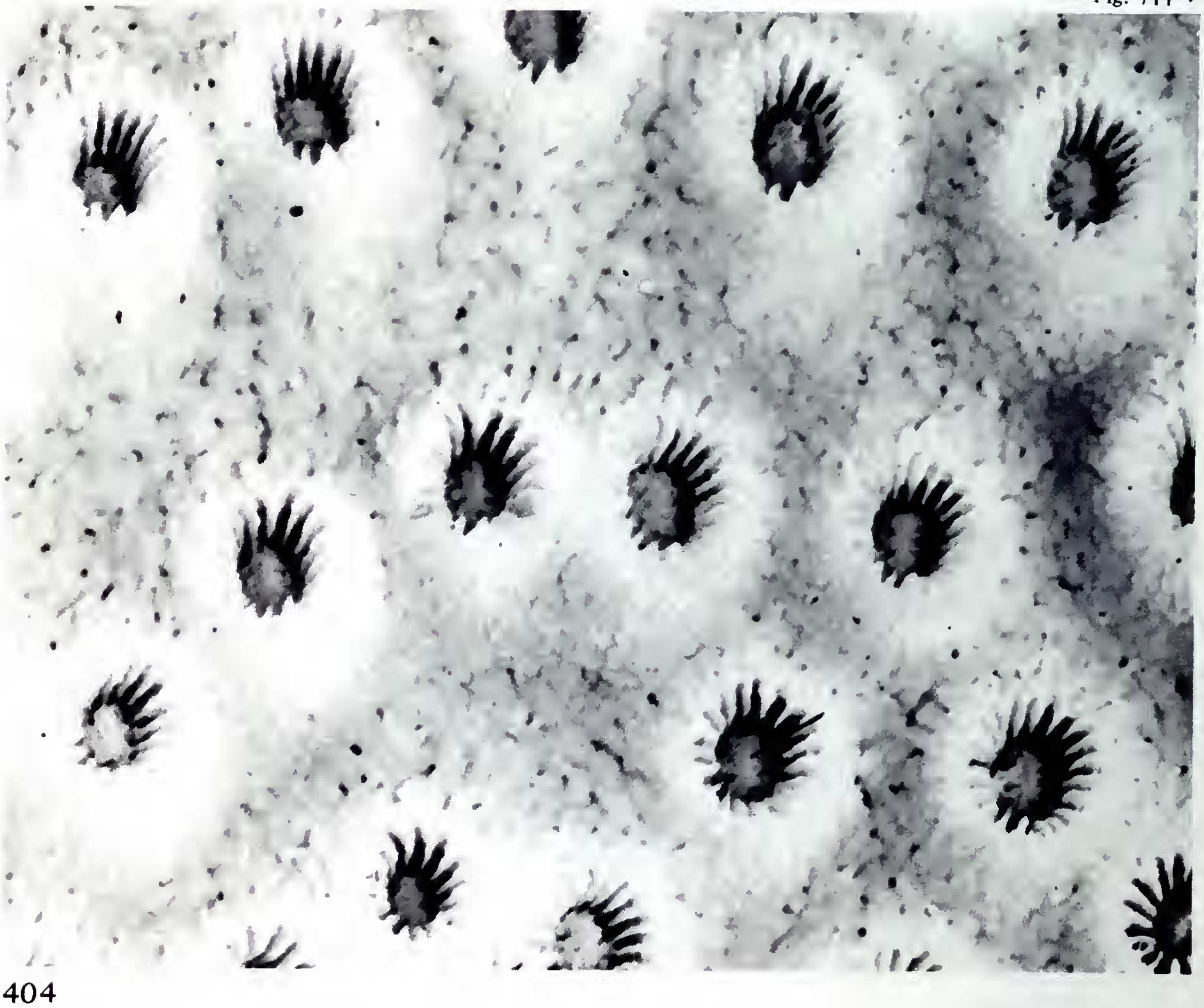


Fig. 710 ▲

Fig. 711 ▼




712


713

The type specimen of *T. conspicua* from Western Australia has slighly larger corallites with more (about 24) septa and boss-like columellae at the frond margins. The synonymy of these species therefore remains tentative.

Distribution

Turbinaria bifrons is known only from tropical Australia and Japan.

Turbinaria radicalis Bernard, 1896

Synonymy

Turbinaria radicalis Bernard, 1896.

Material studied

Anchor Cay, Yorke Island (2 specimens), **Jervis Island, Whitsunday Islands** (2 specimens), **Solitary Islands, Lord Howe Island** (7 specimens).

These localities include collecting stations 147, 156, 192, 237, 249, 253.

Previous records from Eastern Australia

Great Barrier Reef, Bernard (1896); **Solitary Islands**, (as *T. crater*) Veron *et al.* (1974); **Lord Howe Island**, Veron & Done (1979).

Figs. 712, 713 *Turbinaria radicalis* from Lord Howe Island, showing upper and lower surfaces respectively (× 0.7).

Figs. 714-716 *Turbinaria radicalis* from Lord Howe Island, Fig. 716 overlying *Turbinaria mesenteria* (× 2.5).

Fig. 714 ▼

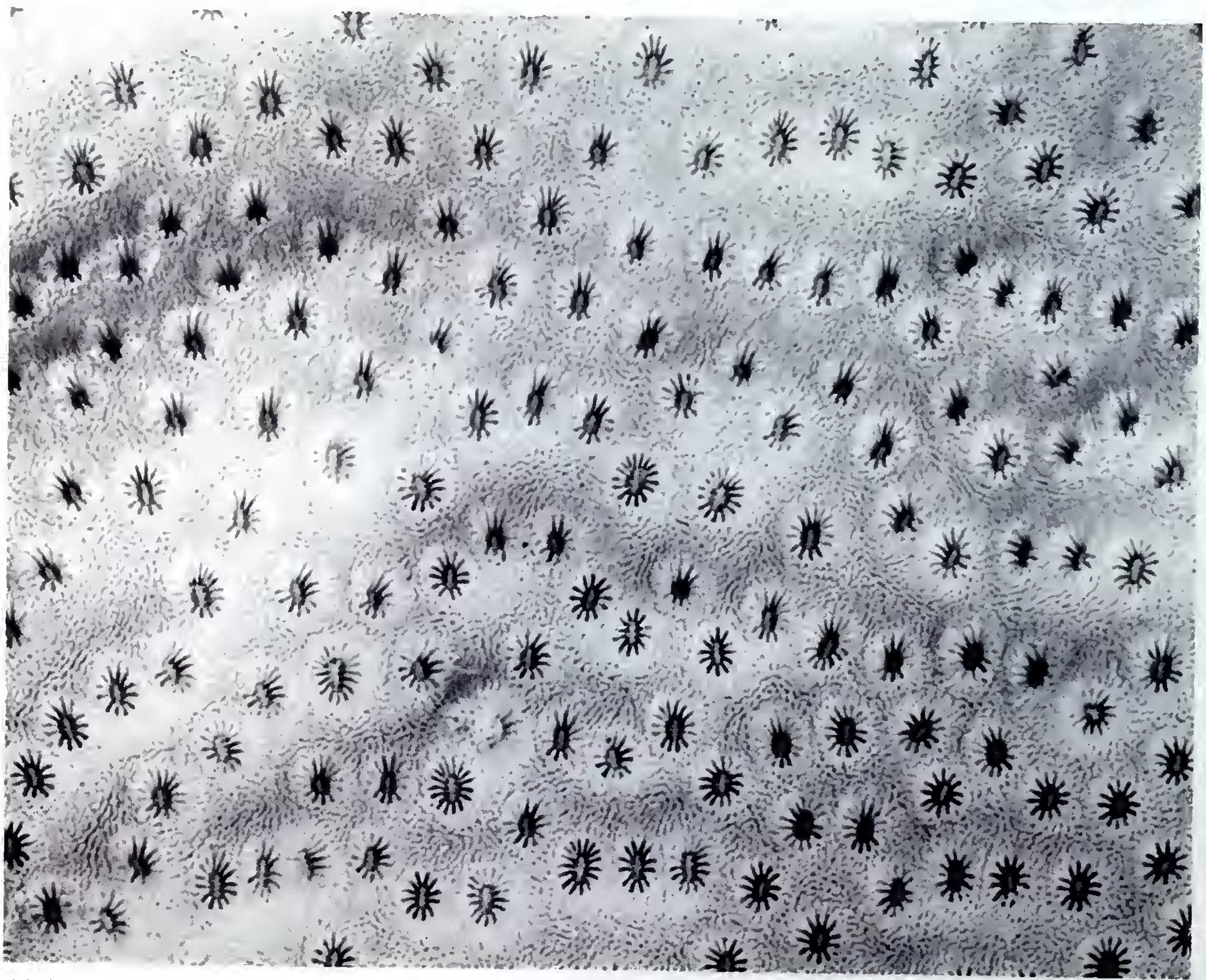


Fig. 715 ▲

Fig. 716 ▼

Characters

Colonies are encrusting or form horizontal plates up to 15 mm thick and 1 m across. They are attached to the substrate by a series of tapering projections or 'rootlets' (Fig. 713) up to 55 mm long and 15 mm thick at their proximal end. These rootlets are irregularly shaped according to the nature of the substrate they penetrate or adhere to and are frequently branched or anastomose. They are entirely made of compact coenosteum and are devoid of corallites. Their proximal surface is frequently encrusted with algae or bryozoa, which do not appear to affect the growth of their tips. The cores of the rootlets are composed of vesicular coenosteum.

Corallites may form irregularly concentric rows on flat laminae but are usually compacted on concave surfaces and widely separated on convex ones. They are never strongly inclined. They are small (2.5-3.5 mm diameter), circular or slightly elliptical and are slightly protuberant, with well defined margins. They contain 12-20 equal, evenly spaced septa, with non-anastomosed sub-vertical inner margins. Columellae are elongate, either single- or tri-ridged, or sometimes taking the form of a series of vertical plates connected perpendicularly to a central ridge. The coenosteum is porous and devoid of ornamentation except for patterns produced by the disposition of the corallites.

Colonies are pale or dark, brown or green, in colour.

Affinities

All but one small specimen of the present series (from the Solitary Islands) have rootlets on the undersurface and are thus readily distinguished from other *Turbinaria* species. Corallites superficially resemble those of some *T. mesenterina* colonies but are not as inclined on the laminae as they normally are in *T. mesenterina* (see Fig. 716) and have only one order of septa. The general growth form is similar only to that of *T. stellulata* which has much larger, more protuberant corallites.

Distribution

Turbinaria radicalis is known only from eastern Australia. It is common at Lord Howe Island (Veron & Done, 1979) where it forms large colonies. It is less abundant at the Solitary Islands where it forms only small, thin coralla and is rare on the Great Barrier Reef.

Turbinaria heronensis Wells, 1958

Synonymy

Turbinaria heronensis Wells, 1958.

Material studied

Palm Islands (5 specimens), **Pompey Complex, Masthead Island** (2 specimens), **Wistari Reef** (2 specimens), **Heron Island** (5 specimens).

These localities include collecting stations 12, 66, 120, 140, 184, 185, 220, 224, 225.

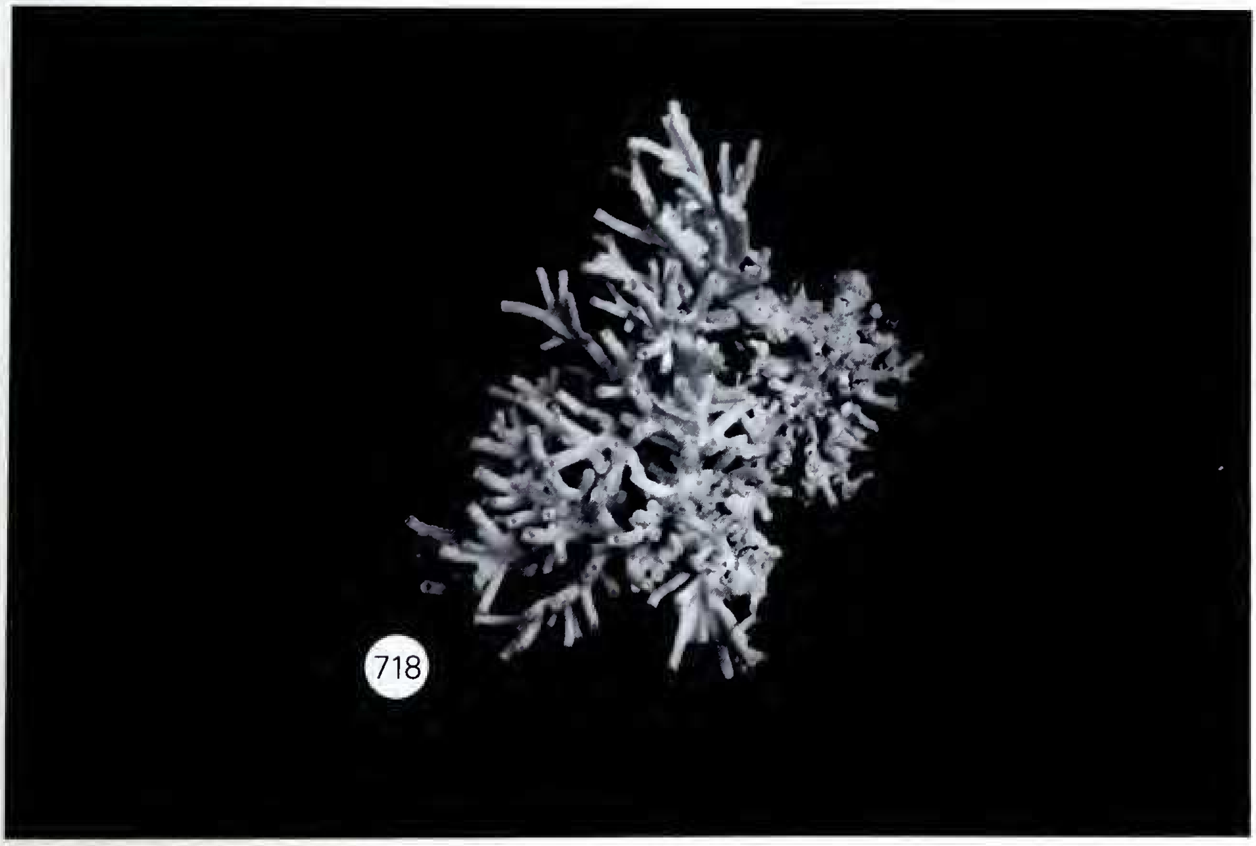
Previous records from Eastern Australia

Low Isles, Whitsunday Islands, Heron Island, Wells (1958).

Figs. 717-720 *Turbinaria heronensis,* Figs. 717, 718 (× 0.5), Figs. 719, 720 (× 2.5).

Figs. 717, 719 From Masthead Island.
Figs. 718, 720 From Barber Island, Palm Islands, collecting station 93.

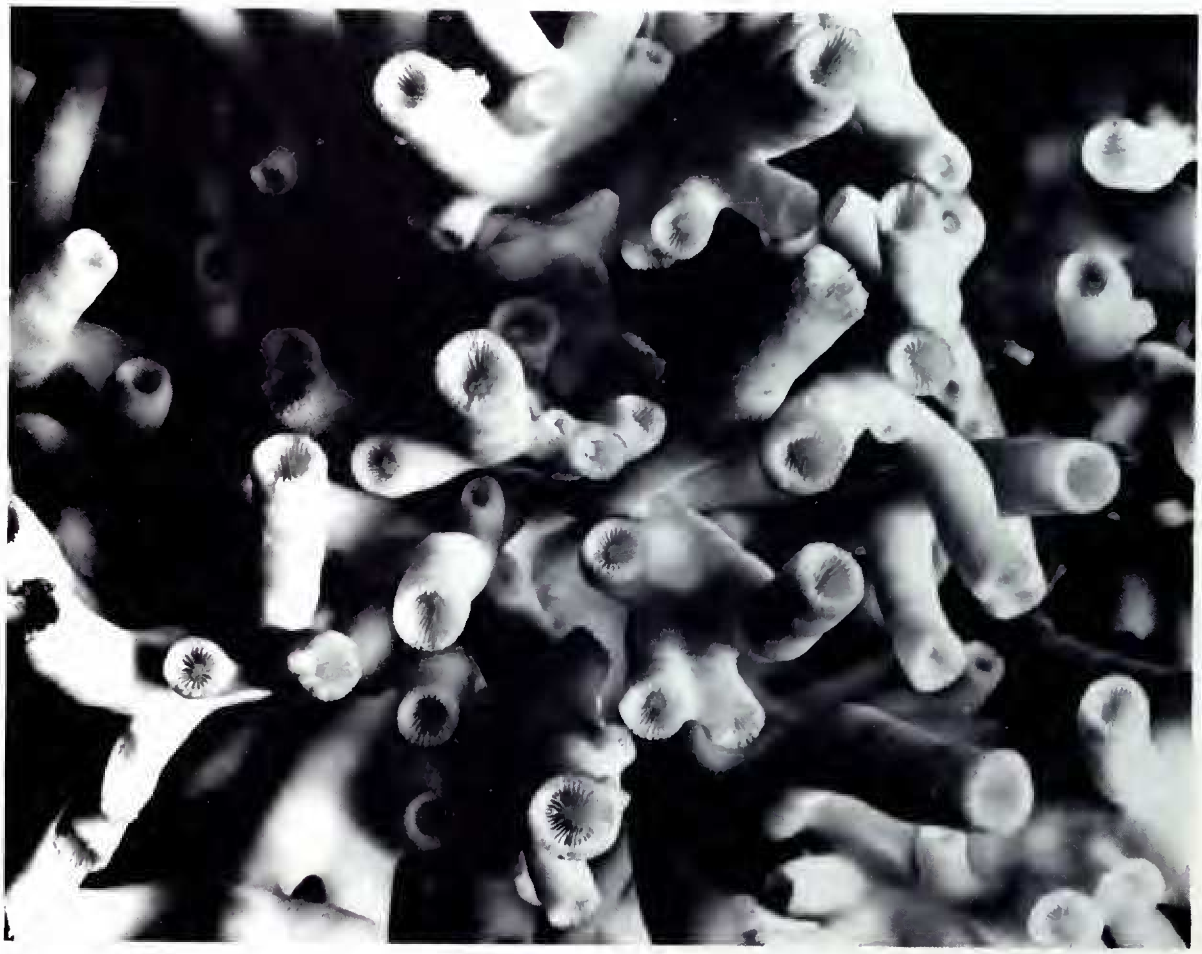
717



718

Fig. 719 ▲

Fig. 720 ▼



Characters

This rare species differs markedly from all other *Turbinaria* in having bushy coralla composed of elongate corallites extending from the margins of anastomosing, fan-shaped fronds (Figs. 856, 857). Large coralla are approximately hemispherical in shape and have a central core of dead skeletal material covered by 10-20 cm of living, irregularly oriented fronds up to 6 cm wide. Each frond is composed of a series of irregularly radiating corallites projecting beyond the margins of the fronds as long tubes supporting lateral buds. Individual corallites are a uniform 3-4 mm diameter and up to 10 cm in length. In some coralla they are fused for all but the last few mm of their length; in more open coralla they may extend up to 5 cm, with or without buds. Budding is very erratic, occurring anywhere on living corallites.

Calices are very deep with septa sloping from the corallite margin to the columella. Only one order of septa can be recognised. These are very thin near the columella but thicker at the margins. A few septa in most corallites anastomose. All are finely granulated. The columellae are spongy and composed of loose folds, or are trabecular. The coenosteum is spongy and has no distinctive ornamentation.

Colonies growing in shallow, clear water are dark brown and/or green in colour. Those growing at >10 m depth are usually a uniform pale brown.

Affinities

This species has no close affinities in *Turbinaria* although its calicular structures are clearly of this genus.

Distribution

Known only from the Great Barrier Reef.

Fig. 721 *Turbinaria heronensis* from Heron Island.

Generic synonymy

Duncanopsammia Wells, 1936c; Wells (1956).

Type species *Dendrophyllia axifuga* Edwards & Haime, 1848a.

Characters of the genus (after Wells, 1956)

Broad, pedunculate, subdendroid, hermatypic colonies formed by extratentacular budding from lower margins of corallites. Corallites basally united by coenosteum; costae reduced to rows of crispate granulations extending over coenosteum. Septa following Pourtalès plan. Columella spongy, deep in calices.

Duncanopsammia is a monospecific genus.

Duncanopsammia axifuga (Edwards & Haime, 1848)

Synonymy

Dendrophyllia axifuga Edwards & Haime, 1848a; Edwards & Haime (1860); Quelch (1886); van der Horst (1922b).

Duncanopsammia axifuga (Edwards & Haime); Wells (1936c); Gardiner & Waugh (1939).

Material studied

Thursday Island, Palm Islands (3 specimens), **Halifax Bay**.

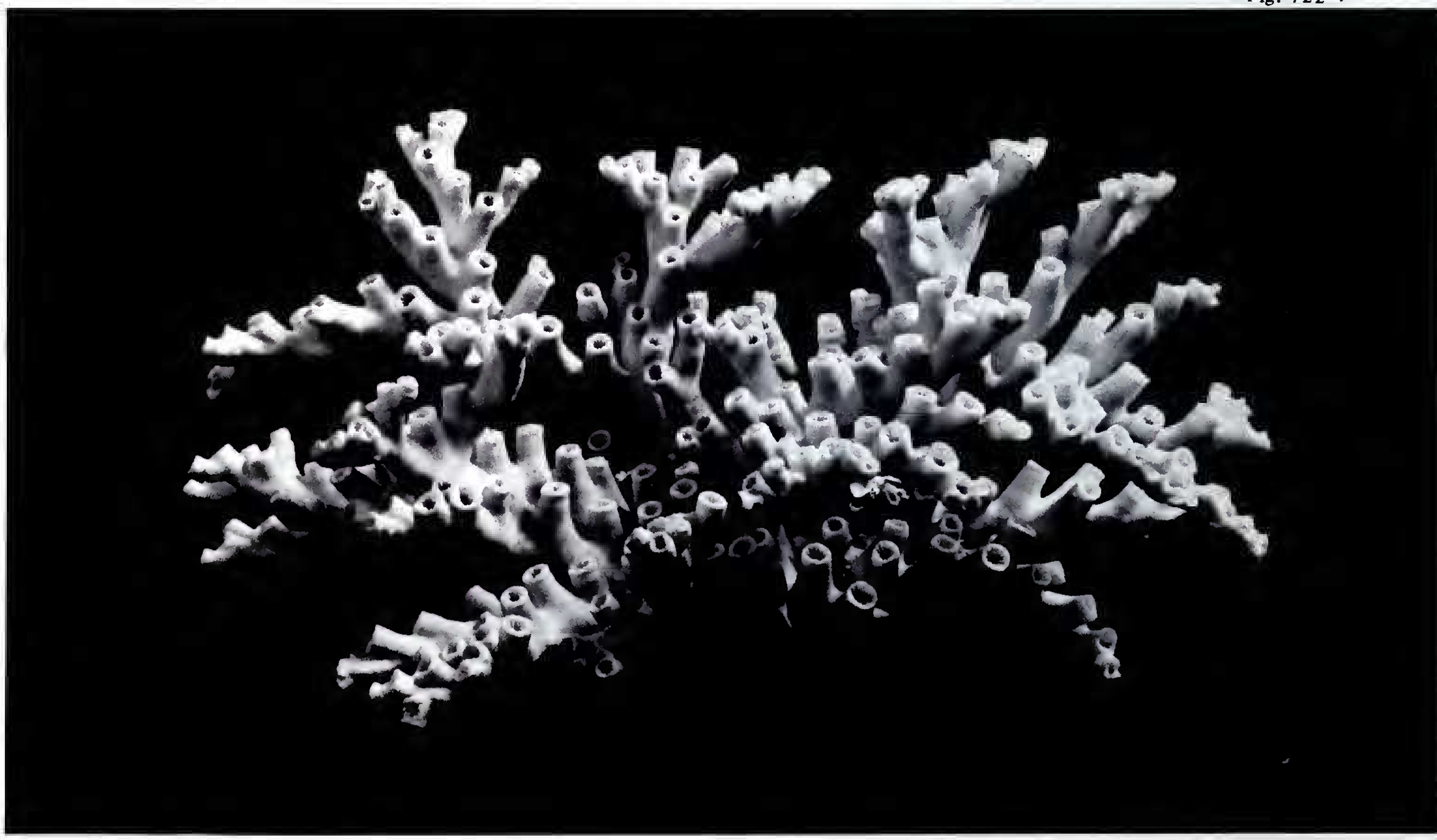
These localities include collecting stations 58, 60.

Fig. 722 *Duncanopsammia axifuga* from the Palm Islands (× 0.3).

Figs. 723, 724 *Duncanopsammia axifuga* (× 5.0).

Fig. 723 From Dido Rock, Palm Islands, collecting station 58.
Fig. 724 From between Orpheus and Fantome Islands, collecting station 60.

Fig. 722 ▼



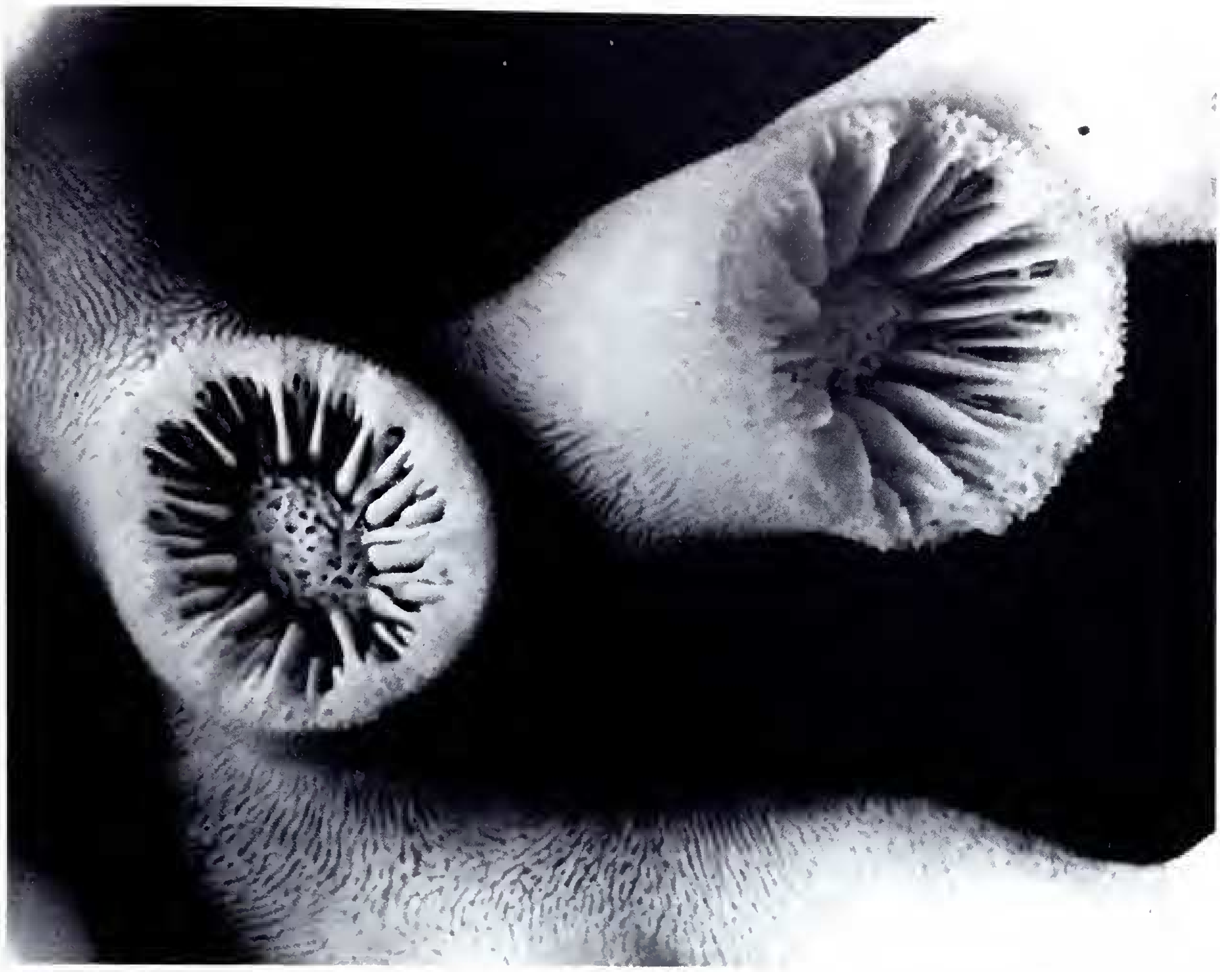


Fig. 723 ▲

Fig. 724 ▼

Previous records from Eastern Australia

Wednesday Island (as *Dendrophyllia axifuga*) Quelch (1886); **Batt Reef, Port Newry,** Wells (1955a).

Characters

Coralla primarily consist of horizontal or obliquely sloping branches, often growing in tiers, supporting elongate, vertical corallites which themselves may develop into sub-branches. Main branches may be up to 2.5 cm thick, mature corallites a uniform 10-14 mm diameter. Individual corallites without buds may extend up to 5 cm from branches. One or more (usually 2-4) extratentacular buds develop at the perimeter of mature corallites and initially grow at a sharp angle before becoming vertical. There is very little anastomosis between corallites although the polyps may grow at irregular heights and distances from each other.

Septa have a strictly hexameral arrangement and follow Pourtalès plan. The first two cycles are similar, the first being only slightly longer and thicker that the second. They are very slightly exsert (giving the perimeter of the calice a wavy appearance) and extend inwards approximately $\frac{2}{3}$ the calice radius. Their inner margins are vertical and are usually thickened, sometimes slightly dentate. The 12 septa of the third cycle are short and usually slightly dentate. Those of the fourth cycle are thinner and longer than those of the third. They may have free inner margins but are usually fused with each other centrally to the free margins of the third cycle, or are fused with the third cycle. They are usually highly dentate and frequently perforate. The fifth cycle is abortive. When formed, these septa are short and fused with those of the fourth cycle.

Fig. 725 *Duncanopsammia axifuga* from the Palm Islands with tentacles extended during the day.

The columellae are large (up to 6 mm diameter), spongy, round or oval and frequently have a directive keel. Twelve equal, low costae may just be distinguished through the coenosteum which is very porous and finely striated, the striations running parallel to the corallite axes. The wall is synapticulothecate with no development of dissepiments.

Polyps are very large and have thick tentacles arranged in 2 irregular rows of approximately 24 each. The stomodaeum is conical or tubular and may project beyond the calicular cavity. Polyps are bright green, the coenosarc a dark brown.

Duncanopsammia axifuga is rarely found on reefs. It normally occurs in relatively deep water, on a horizontal sand or rubble substrate.

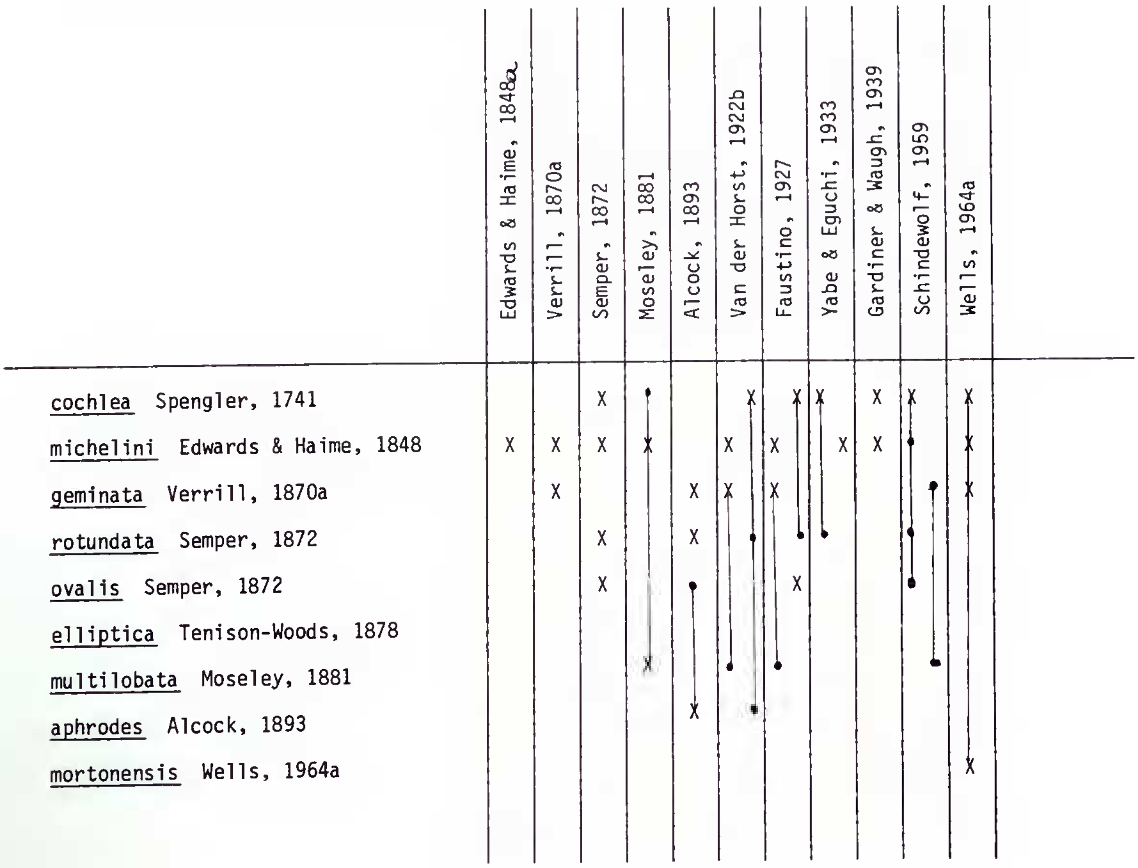
Affinities

Duncanopsammia shows closest affinity to the ahermatypic *Dendrophyllia* and *Tubastraea.* Septa are arranged according to Pourtalès plan and the pattern of budding is similar. It resembles *Turbinaria* in being hermatypic and all four of these genera have in common similar synapticulothecate walls, similar columellae and similar porous coenosteum.

Distribution

Known only from the tropical Australian coast and Indonesia.

Fig. 726 The synonymy of nominal species of *Heteropsammia* according to the authors indicated. Species names considered valid by each author are indicated by a cross. Synonyms are indicated by a dot and joining line.



Generic synonymy

Heteropsammia Edwards & Haime, 1848a.

Type Species *Heteropsammia michelini* Edwards & Haime, 1848a.

Characters (after Wells, 1956, slightly altered)

Solitary, or colonial with up to 7 calices resulting from mono- or distomodaeal intratentacular budding, free, base enclosing tube of commensal sipunculid. Wall thick and spongy; costae reduced to multiple rows of crispate granulations, becoming labyrinthine over base. Septa following Pourtalès plan, lower cycles thick and spongy. Columella well developed.

Taxonomic history

The taxonomic history of the nine nominal species of *Heteropsammia* is summarised in Fig. 726. Edwards & Haime (1848a) were apparently unaware of the earlier description of Spengler's *Madrepora cochlea*, but listed both species (*cochlea* and *michelini*) in 1860.

In his original description of *H. geminata* from Burma, Verrill (1870a) noted that '*H. michelinii [sic]* appears to differ from *H. geminata* not only in dividing less freely, but in its smaller cup and a different arrangement of the septa, those of the three first cycles being described as about equal, while in *H. geminata* those of the third cycle are very small. The columella in the latter appear to be much less developed'. The locality is not recorded.

Moseley (1881) noted that his *H. multilobata* 'differs from *Heteropsammia michelini* in no point of importance except in being compound'. Moseley's specimens had 5-7 calices and are thus outside the range of variation of the present series. However, he considered the three species, *H. cochlea*, *H. michelini* and *H. multilobata* were clearly linked. Van der Horst (1922b) placed *H. multilobata* in synonymy with *H. geminata* which he separated from *H. michelini* claiming that the latter was monocentric 'with very rare exception'. He claimed that Tenison-Woods, who included polycentric specimens in his *H. michelini*, 'had these two species mixed together' but later (1926) appeared to change his mind.

The conclusions of van der Horst were largely accepted by Faustino (1927) and Yabe and Eguchi (1933a) and the genus was not restudied in detail unti Schindewolf's (1958) account of coral and sipunculid symbiosis. Schindewolf concentrated his taxonomic observations on the number of calices per corallum, the number of septal orders and the ratio of the maximum and minimum diameters of the corallum base. He concluded that there were no grounds for differentiating *H. cochlea, H. michelini, H. rotundata* and *H. ovalis* (a fossil) nor for differentiating *H. geminata* and *H. multilobata* and concluded that all appeared to represent a single species with the latter two at the extreme of the range, having multiple calices.

The remaining species have received very little discussion in the literature. *Heteropsammia aphrodes* is only distinguished by its small base, the diameter of the calice being 'not much less than that of the base—the basal "spur" excluded' (Alcock, 1893). Wells' (1964b) description of *H. moretonensis* from Moreton Bay hardly differs from *H. elliptica* Tenison-Woods from the vicinity of Sydney. Wells noted that his species differs from *H. michelini* by its 'subcuneform corallum and non-inflated base'.

Heteropsammia cochlea (Spengler, 1781)

Synonymy

Madrepora cochlea Spengler, 1781.

Heteropsammia michelini Edwards & Haime, 1848a; Edwards & Haime (1860); Semper (1872); Tenison-Woods (1878, 1880a); Moseley (1881); van der Horst (1922b, 1926); Gardiner & Waugh (1939); Yabe & Eguchi (1932); Boschma (1959); Scheer & Pillai (1974).

Heteropsammia cochlea (Spengler); Edwards & Haime (1851c, 1860); Bouvier (1895); van der Horst (1922b, 1926); Faustino (1927); Yabe & Eguchi (1933); Gardiner & Waugh (1939); Schindewolf (1958); Cheng (1971).

Heterocyathus cochlea (Spengler); Gray (1849).

Heterocyathus eupsammides Gray, 1849.

Heteropsammia geminata Verrill, 1870a; Alcock (1893); van der Horst (1922b); Faustino (1927).

Heteropsammia elliptica Tenison-Woods, 1878.

?*Heteropsammia multilobata* Moseley, 1881; Fowler (1890).

Heteropsammia aphrodes Alcock, 1893; Harrison (1911).

Heteropsammia moretonensis Wells, 1964b.

This study indicates that there are no firm grounds for distinguishing any of the nominal species of *Heteropsammia*. All forms of the genus except *H. multilobata* (with 5-7 calices) have been observed underwater and collected in large numbers over a wide range of environments along the east Australian coast. However, there has never been any evidence that more than one species is present in any one biotope, although there is always a wide range of forms in each collection usually corresponding to more than one nominal species. Furthermore,

Figs. 727, 728 *Heteropsammia cochlea* (× 1.0).

Fig. 727 Immature stages from Lizard Island.
Fig. 728 The range of mature forms normally found within the same biotope. From Wistari Reef.

there is an obvious correlation between growth form and substrate. Thus, large coralla of the *geminata* form are predominant on sand; *cochlea / michelini / rotundata / ovalis* forms are found on soft sand or mud and *elliptica / moretonensis* forms are found on soft ooze. There would appear only a very remote possibility that the latter forms are a distinct species restricted to very soft substrates. As noted above, some of Moseley's *H. multilobata* have more calices than any specimens of the present series but Moseley himself, as well as subsequent authors, doubted the validity of this species as many intermediate forms having fewer corallites were indistinguishable from *H. cochlea / michelini* forms.

Heteropsammia and other mobile species are compared with their fossil counterparts by Gill & Goates (1977).

Material studied

Bramble Cay to **Low Isles** (115 specimens), **Lizard Island** (63 specimens), **Holbourne Island** (28 specimens), **Wistari Reef** (51 specimens).

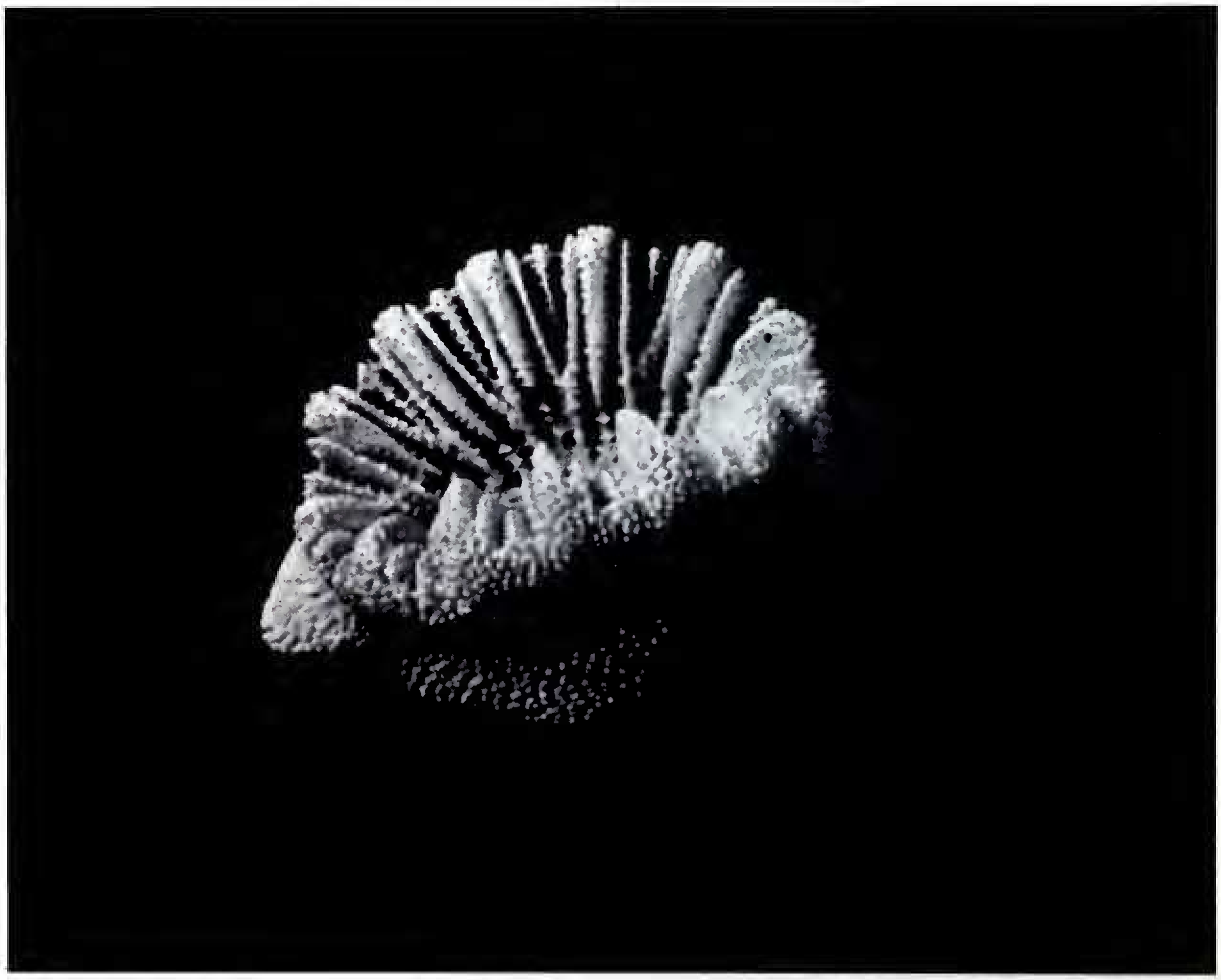
Previous records from Eastern Australia

Lizard Island, Goreau & Yonge (1968); **Moreton Bay** (as *H. moretonensis*) Wells (1964b) (as *H. moretonensis*) Stephenson *et al.* (1970); 'tropics of **N.E. Australia',** Tenison-Woods (1878, 1880a); **Port Jackson, Manning River, Sydney Harbour** (as *H. elliptica*) Tenison-Woods (1878).

Characters

The present series exhibits a very wide range of variation which is closely related to the nature of the substrate in which it occurs. All colonies are free-living. Settlement initially occurs on small (3-10 mm long) gastropod shells of various

Fig. 729 *Heteropsammia cochlea* from near Bewick Island (× 2.0).



species. By subsequent growth, the corallum engulfs the shell, the shape of which can usually be seen in all but the largest specimens. Before the shell is completely engulfed, however, it becomes occupied by the sipunculid worm *Aspidosiphon corallicola*. During subsequent growth the sipunculid maintains a horizontal tube within the coral coenosteum leading from the gastropod shell to an opening in the side of the coral. As the coral grows the tube is extended in an arc around the gastropod. Apart from the main opening the tube is connected to the outside of the coral by a series of pores which Moseley (1881) originally suggested had a respiratory function. The worm is readily able to move the coral by periodically extending and contracting its proboscis.

This presumably symbiotic relationship between sipunculid and coral has been discussed many times, most recently and comprehensively by Schindewolf (1958) and Goreau and Yonge (1968). It remains to be noted here that the shape of individual coralla are largely the result of the shape of the original gastropod shell, the position on the shell of the settlement of the juvenile coral, the control of coral coenosteum growth exercised by the sipunculid and the nature of the substrate on which the coral lives. Every specimen of some hundreds of *Heteropsammia* observed in the present study contained both a gastropod shell and a sipunculid, and thus it appears likely that the coral cannot have a prolonged independent existence.

Coralla usually have a flat under-surface at one end of which is the circular opening of the worm passage. Just above this opening, and frequently connected to it by a groove, is often a second opening made by a solitary boring bivalve (see Arnaud & Thomassin, 1976). Viewed from above, the base of the corallum is sub-circular in shape with a projection in one quarter indicating the position of the enclosed gastropod. One calice only may be present, either circular in outline or laterally constricted to form a figure-of-eight. Further constriction results in the formation of two calices and some coralla may have further lateral buds.

The configuration of the septa has never been clearly described although several nominal species are distinguished primarily on septal structures. The basic hexameral Pourtalès plan is clearly visible in very young specimens. First and second cycle septa, six of each, are nearly equal and extend to the columella. The 12 third cycle septa are less exsert, thinner and about half as long. The 24 fourth cycle septa, which are visible in all but the smallest calices, are thinner and non-exsert and longer than those of the third cycle in front of which they usually anastomose. In larger calices, the first and second cycles become indistinguishable and in fully mature calices the first three cycles may be hardly distinguishable. In the latter case 6 complete cycles may be present and usually the pattern of anastomoses seen in smaller calices is less distinguishable. The combined septa of mature calices usually make up three concentric circles of lobes. The outer circle is composed of the exsert outer margins of the first or first and second cycle septa. The second circle is composed of high lobes above the inner margins of third and/or fourth cycle septa. The inner circle is composed of pali and paliform dentations. These seldom form a distinct crown and are frequently absent. All septa are highly granulated, porous and perforate, with synapticulae frequently arranged in layers. The theca is likewise synapticulothecate and there is often no distinct demarkation between the thecal rim and septa. Costae are very reduced. The columellae are foliaceous or spongy, usually conspicuous, but seldom high.

Zooxanthellae may be present or absent from the polyps. The latter are expanded only at night.

Growth form variation

The growth form of *H. cochlea* varies markedly with variation in the nature of the substrate.

Heteropsammia cochlea from sandy substrates

Coralla may be up to 20 mm maximum diameter. Large coralla frequently have two or more calices, but if only one is present, this has the figure-of-eight outline noted above. All coralla have broad, flat bases; polyps usually contain zooxanthellae.

This ecomorph is frequently associated with *Trachyphyllia geoffroyi, Diaseris distorta* and *Cycloseris cyclolites.*

Heteropsammia cochlea from sandy substrates (ecomorph *elliptica*).

Coralla are usually small and monocentric. The gastropod on which settlement occurs is frequently very small and only covered with a thin layer of coenosteum. Bases are frequently narrow and in some cases reduced to a point or keel.

This ecomorph is usually found in association with *Heterocyathus aequicostatus* Edwards & Haime in the tropics and ranges at least as far south as Sydney where it is probably ahermatypic.

Distribution

Widely distributed throughout the Indian Ocean from the east coast of Africa and the Persian Gulf east to the Coral Sea.

Fig. 730	*Pavona cactus* from Eclipse Island, Palm Islands.
Fig. 731	*Pavona decussata* from Aureed Island.
Fig. 732	*Pavona explanulata* from Lord Howe Island.
Fig. 733	*Pavona explanulata* (above) and *Pavona minuta* (below) from Bramble Cay.
Fig. 734	*Pavona clavus* from Dungeness Reef.
Fig. 735	*Pavona varians* from Haselwood Island, Whitsunday Islands.
Fig. 736	*Pavona venosa* from Dungeness Reef.
Fig. 737	*Pavona maldivensis* from Heron Island.
Fig. 738	*Leptoseris explanata* from Eclipse Island, Palm Islands.
Fig. 739	*Leptoseris scabra* from Anchor Cay.
Fig. 740	*Leptoseris hawaiiensis* from Dungeness Reef.
Fig. 741	*Leptoseris mycetoseroides* from Pearce Cay.
Fig. 742	*Leptoseris tenuis* from Big Mary Reef.
Fig. 743	*Leptoseris yabei* from Big Mary Reef.
Fig. 744	*Leptoseris yabei* from Yorke Island.
Fig. 745	*Gardineroseris planulata* from Bramble Cay.
Fig. 746	*Coeloseris mayeri* from Dungeness Reef.
Fig. 747	*Pachyseris rugosa* from Aureed Island.
Fig. 748	*Pachyseris speciosa* from Yorke Island.
Fig. 749	*Pseudosiderastrea tayamai* from Hook Island, Whitsunday Islands.
Fig. 750	*Coscinaraea exesa* from the Swain Reefs, with polyps extended at night.
Fig. 751	*Coscinaraea columna* from Lord Howe Island.
Fig. 752	*Coscinaraea wellsi* from Lord Howe Island.
Fig. 753	*Cycloseris cyclolites* from Lizard Island.
Fig. 754	*Heliofungia actiniformis* from the Swain Reefs.
Fig. 755	*Fungia fungites* from the Palm Islands (Photo: J. Barnett).
Fig. 756	*Fungia moluccensis* from Hook Island, Whitsunday Islands.
Fig. 757	Anthocauli of *Fungia fungites.*
Fig. 758	*Podabacia* cf. *edwardsi* from Fantome Island, Palm Islands.
Fig. 759	*Galaxea* cf. *astreata* from Fantome Island, Palm Islands.
Fig. 760	*Galaxea* cf. *astreata* from Jervis Reef, with tentacles extended during the day.
Fig. 761	*Galaxea fascicularis* from Jervis Reef.
Fig. 762	*Galaxea fascicularis* from Gould Reef.
Fig. 763	*Acrhelia horrescens* from Maer Island, Murray Islands.
Fig. 764	*Merulina ampliata* from E of Murray Islands.
Figs. 765, 766	*Clavarina triangularis* from Big Mary Reef.
Fig. 767	*Blastomussa merleti* from Lizard Island.
Figs. 768, 769	*Blastomussa wellsi* from Lizard Island.
Fig. 770	*Cynarina lacrymalis* from the Swain Reefs.
Fig. 771	*Scolymia* cf. *vitiensis* from E of Murray Islands.
Fig. 772	*Scolymia* cf. *vitiensis* from the Palm Islands.
Fig. 773	*Scolymia* cf. *vitiensis* from the Murray Islands.
Fig. 774	*Scolymia* cf. *vitiensis* from Lord Howe Island.
Fig. 775	*Scolymia australis* from Tipara Lighthouse, South Australia (Photo: K. L. Branden).

Figs. 776, 777 *Acanthastrea echinata* from Hook Island, Whitsunday Islands.
Fig. 778 *Acanthastrea echinata* from Heron Island (Photo: J. Barnett).
Figs. 779, 780 *Acanthastrea hillae* from Lord Howe Island (Fig. 779, Photo: J. Barnett).
Fig. 781 *Acanthastrea hillae* (left) and *Acanthastrea bowerbanki* (right) from Lord Howe Island.
Figs. 782-784 *Acanthastrea bowerbanki* from Lord Howe Island (Fig. 784, Photo: J. Barnett).
Figs. 785-790 *Lobophyllia hemprichii* from Wistari Reef, Figs. 788-790 showing adjacent or compound colonies with differing polyp morphologies (Figs. 788, 790, Photo: J. Barnett).
Fig. 791 *Lobophyllia hemprichii* (left) and *Lobophyllia corymbosa* (right) from Wistari Reef.
Fig. 792 *Lobophyllia corymbosa* from Hook Island, Whitsunday Islands.
Fig. 793 *Lobophyllia corymbosa* from Wistari Reef.
Fig. 794 *Lobophyllia pachysepta* from Haselwood Island, Whitsunday Islands.
Fig. 795 *Lobophyllia hattai* from Gould Reef (Photo: J. Barnett).
Fig. 796 *Symphyllia recta* from Gould Reef (Photo: J. Barnett).
Fig. 797 *Symphyllia* cf. *radians* from Gould Reef (Photo: J. Barnett).
Fig. 798 *Symphyllia agaricia* from Heron Island (Photo: J. Barnett).
Fig. 799 *Symphyllia* cf. *valenciennesi* from Anchor Cay.
Fig. 800 *Echinophyllia aspera* from Heron Island (Photo: J. Barnett).
Figs. 801, 802 *Echinophyllia aspera* from Hook Island, Whitsunday Islands. (Fig. 792, Photo: J. Barnett).
Fig. 803 *Echinophyllia orpheensis* from Yorke Island.
Fig. 804 *Echinophyllia orpheensis* from Hook Island, Whitsunday Islands.
Fig. 805 *Echinophyllia echinata* from Ashmore Reef.
Fig. 806 *Echinophyllia echinoporoides* from Warrior Island.
Figs. 807, 808 *Oxypora lacera* from Dewar Island, Murray Islands.
Fig. 809 *Oxypora lacera* from Bushy Island (Photo: J. Barnett).
Fig. 810 *Oxypora lacera* from Jervis Reef.
Fig. 811 *Mycedium elephantotus* from Lord Howe Island (Photo: J. Barnett).
Fig. 812 *Mycedium elephantotus* from Heron Island (Photo: J. Barnett).
Fig. 813 *Mycedium elephantotus* from Gould Reef (Photo: J. Barnett).
Fig. 814 *Pectinia lactuca* from the Murray Islands.
Fig. 815 *Pectinia lactuca* from Hook Island, Whitsunday Islands.
Fig. 816 *Pectinia lactuca* from Gould Reef.
Fig. 817 *Pectinia paeonia* from Bramble Cay.
Fig. 818 *Pectinia paeonia* from Gould Reef (Photo: J. Barnett).
Fig. 819 *Pectinia alcicornis* from Maer Island, Murray Islands.
Fig. 820 *Pectinia alcicornis* from Big Mary Reef.
Fig. 821 *Pectinia alcicornis* from Hook Island, Whitsunday Islands.
Fig. 822 *Euphyllia (Euphyllia) glabrescens* (top right), *Euphyllia (Fimbriaphyllia) ancora* (left) and *Euphyllia (Fimbriaphyllia) divisa* (bottom right), all from the same biotope from the Swain Reefs.
Fig. 823 *Euphyllia (Euphyllia) glabrescens* from the Swain Reefs (Photo: J. Barnett).
Fig. 824 *Euphyllia (Fimbriaphyllia) divisa* from the Swain Reefs with tentacles partly retracted (Photo: J. Barnett).
Fig. 825 *Euphyllia (Fimbriaphyllia) divisa* from Maer Island, Murray Islands.
Fig. 826 *Euphyllia (Fimbriaphyllia) divisa* from Thursday Island with tentacles fully extended.
Fig. 827 *Euphyllia (Fimbriaphyllia) ancora* from the Palm Islands.
Fig. 828 *Euphyllia (Fimbriaphyllia) ancora* from Gould Reef (Photo: J. Barnett).
Fig. 829 *Euphyllia (Fimbriaphyllia) ancora* from Maer Island, Murray Islands.
Figs. 830, 831 *Catalaphyllia jardinei* from Hook Island, Whitsunday Islands.
Fig. 832 *Plerogyra sinuosa* from Wistari Reef.
Fig. 833 *Plerogyra sinuosa* from Bramble Cay.
Fig. 834 *Plerogyra sinuosa* from Parker Reef.
Fig. 835 *Physogyra lichtensteini* from Yorke Island.
Fig. 836 *Physogyra lichtensteini* from Bushy Island with tentacles extended at night (Photo: J. Barnett).
Fig. 837 *Turbinaria peltata* from Lord Howe Island.
Fig. 838 *Turbinaria peltata* from Ribbon Reef.
Fig. 839 *Turbinaria peltata* from Lizard Island with polyps extended during the day.
Fig. 840 *Turbinaria peltata* from Lord Howe Island with polyps partly extended.
Fig. 841 *Turbinaria mesenterina* from Newman Reef.
Fig. 842 *Turbinaria mesenterina* (bottom colonies) and *T. bifrons* (above) from Geoffrey Bay, Magnetic Island.
Fig. 843 *Turbinaria mesenterina* (brown colony) intermixed with *Turbinaria reniformis* (central yellow colony) from Pandora Reef.
Fig. 844 *Turbinaria mesenterina* (right) and *Turbinaria reniformis* (left) from Pandora Reef.
Fig. 845 *Turbinaria reniformis* from Ashmore Reef.
Fig. 846 *Turbinaria frondens* from Bramble Cay.
Figs. 847-849 *Turbinaria frondens* from Lord Howe Island.
Fig. 850 *Turbinaria stellulata* from Bramble Cay.

Fig. 851	*Turbinaria stellulata* from Pearce Cay.
Fig. 852	*Turbinaria stellulata* from Magnetic Island.
Fig. 853	*Turbinaria stellulata* from E of Murray Islands showing an explanate growth form.
Fig. 854	Adjacent colonies of *Turbinaria reniformis* (left) and *Turbinaria stellulata* (right).
Fig. 855	*Turbinaria bifrons* from Heron Island.
Figs. 856, 857	*Turbinaria heronensis* from Heron Island.

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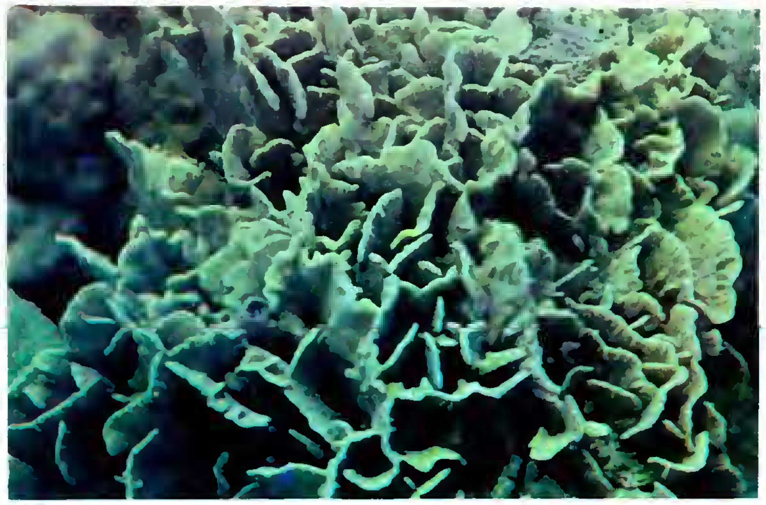

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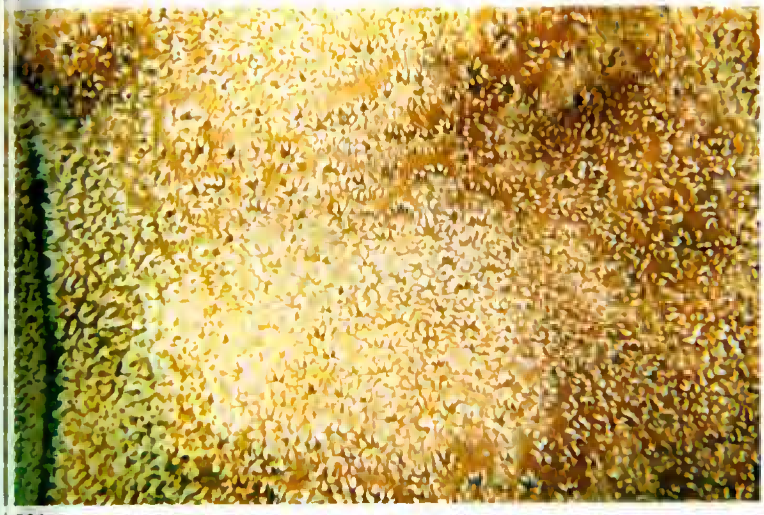

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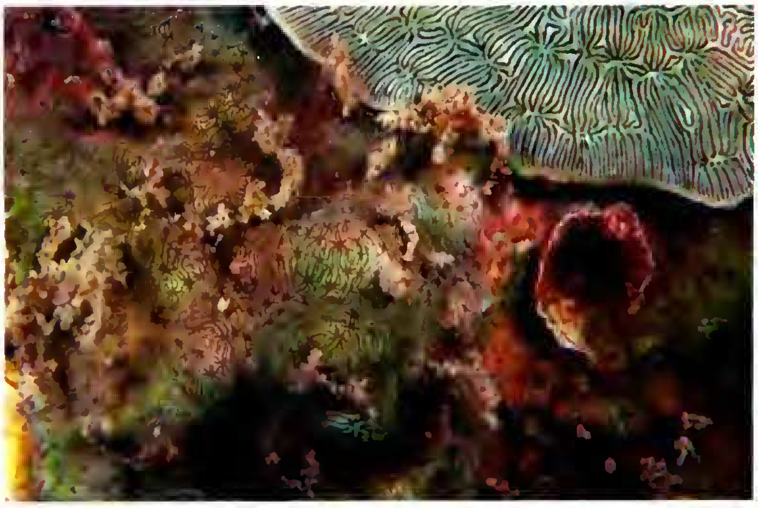

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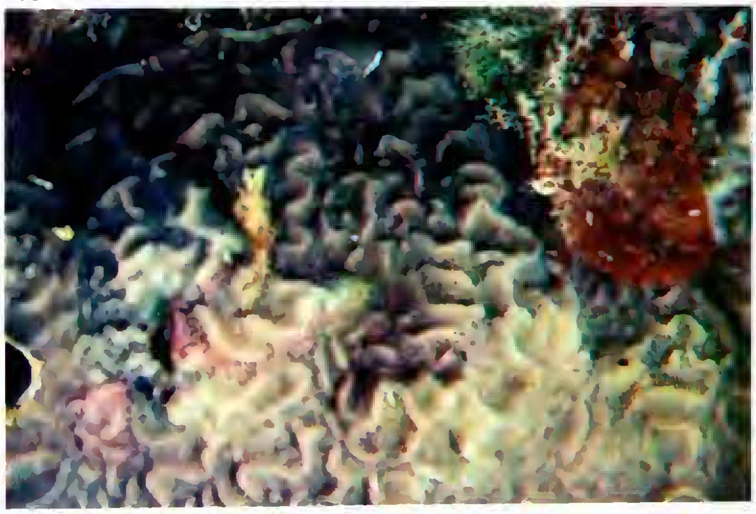

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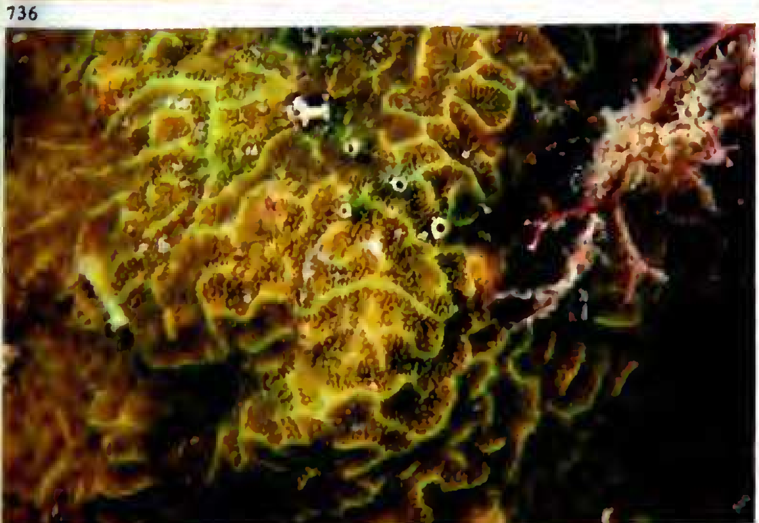

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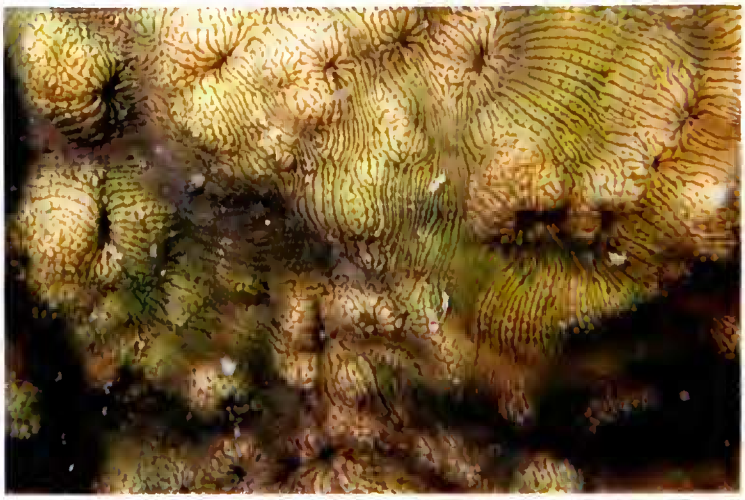

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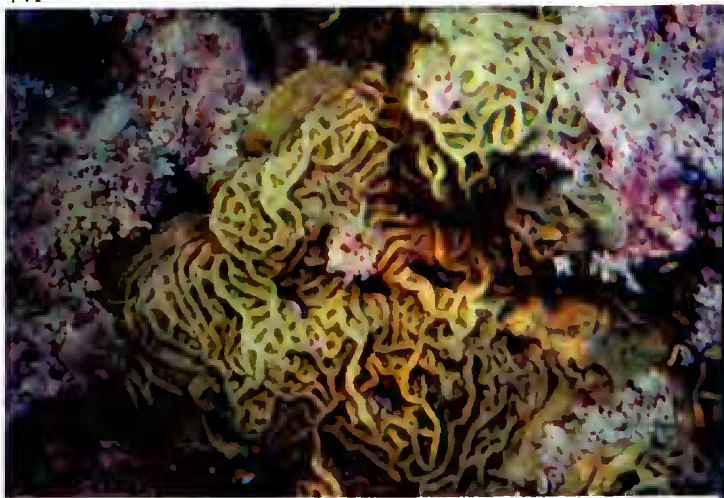

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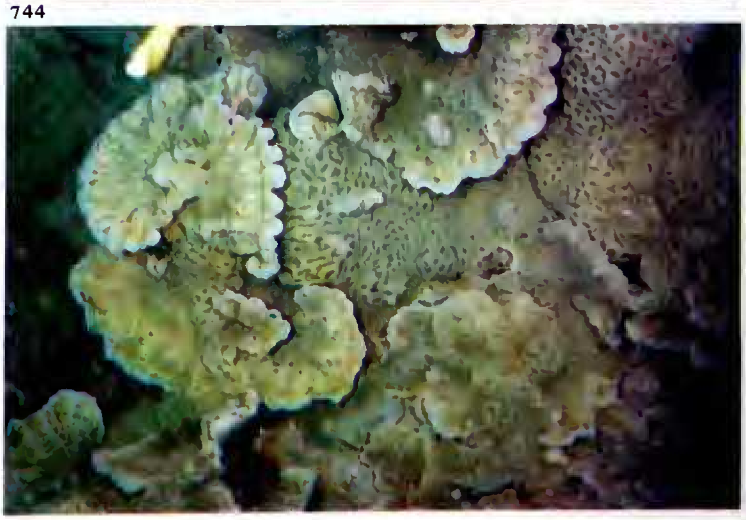

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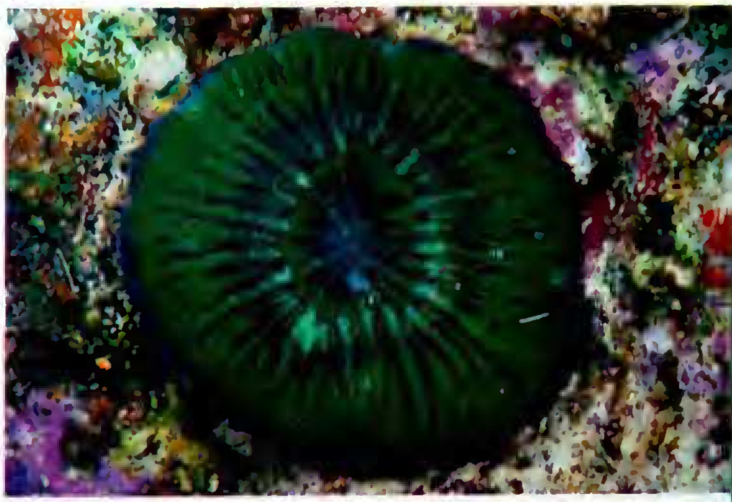

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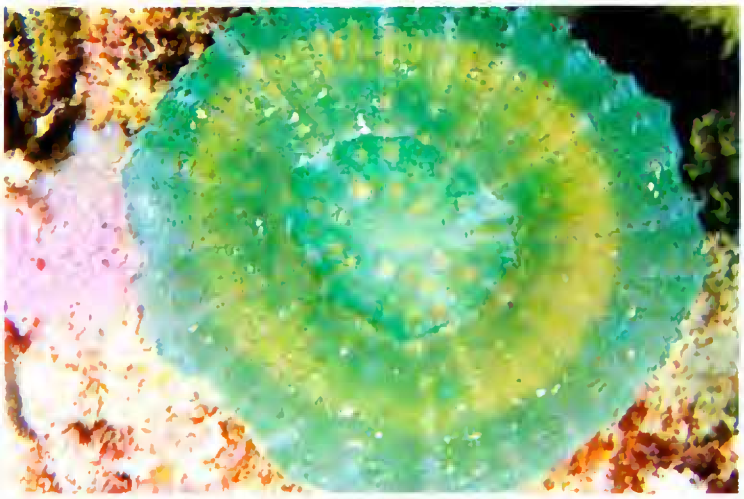

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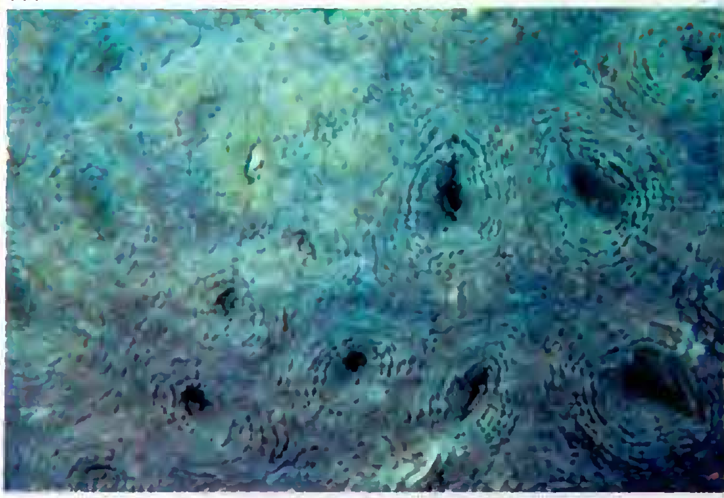

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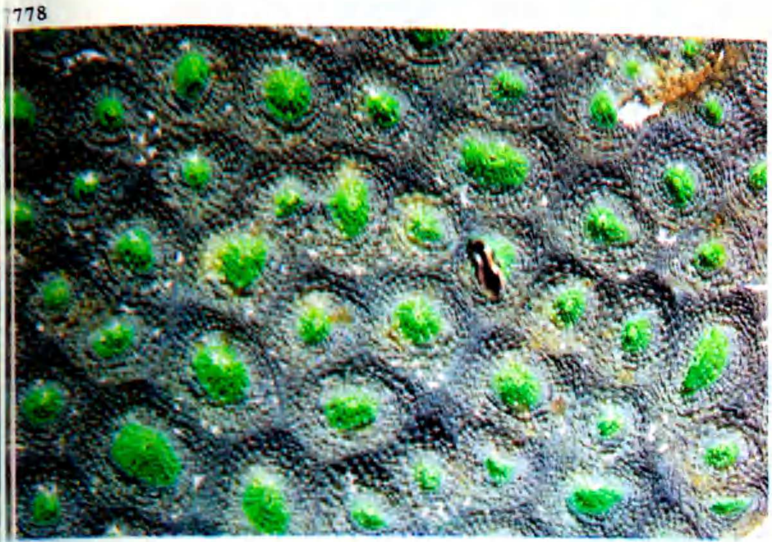

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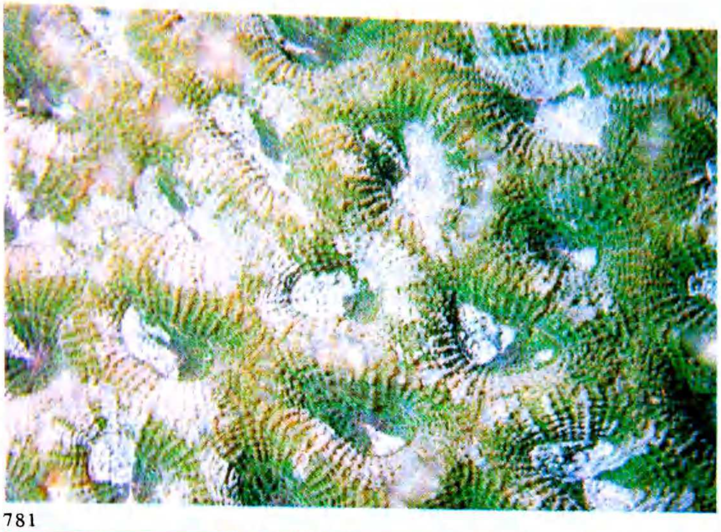

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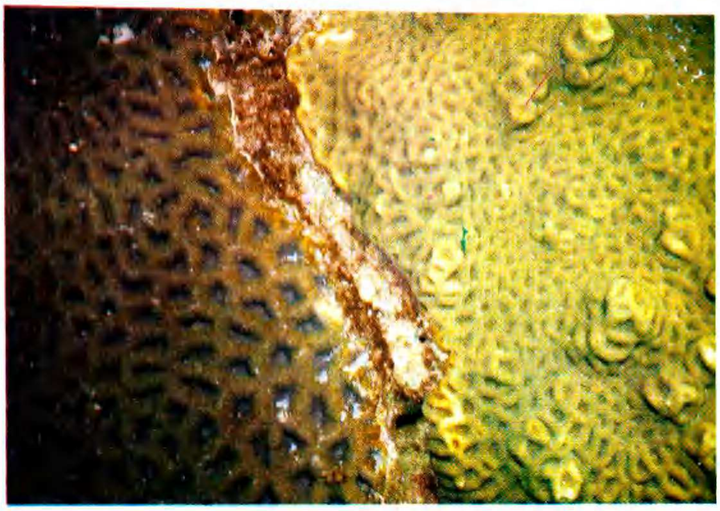

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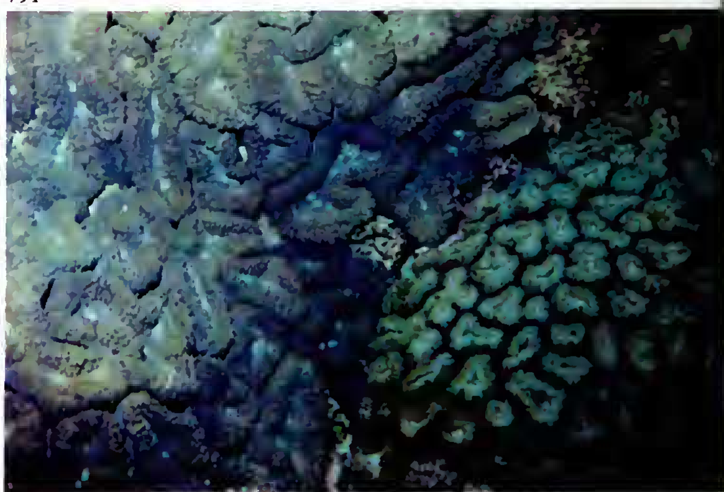

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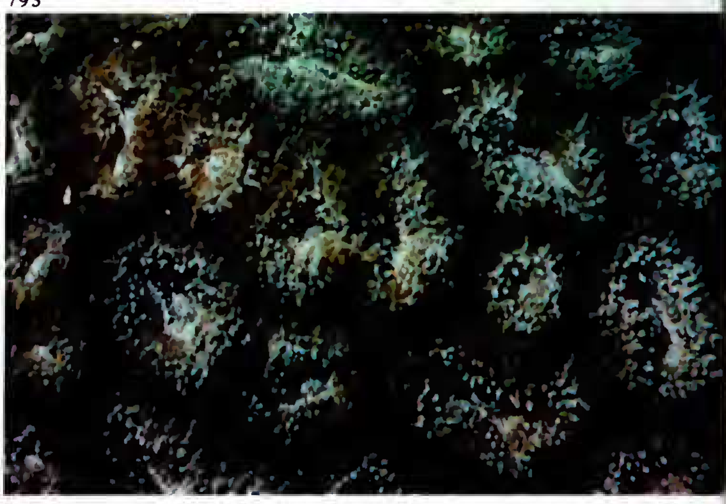

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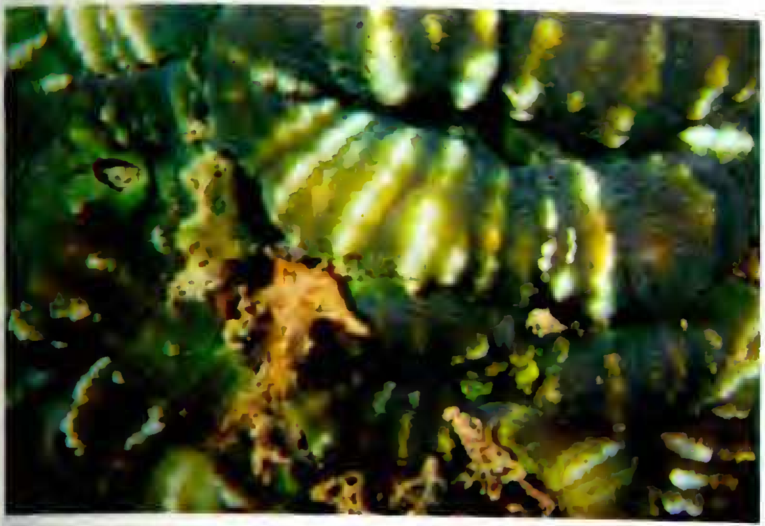
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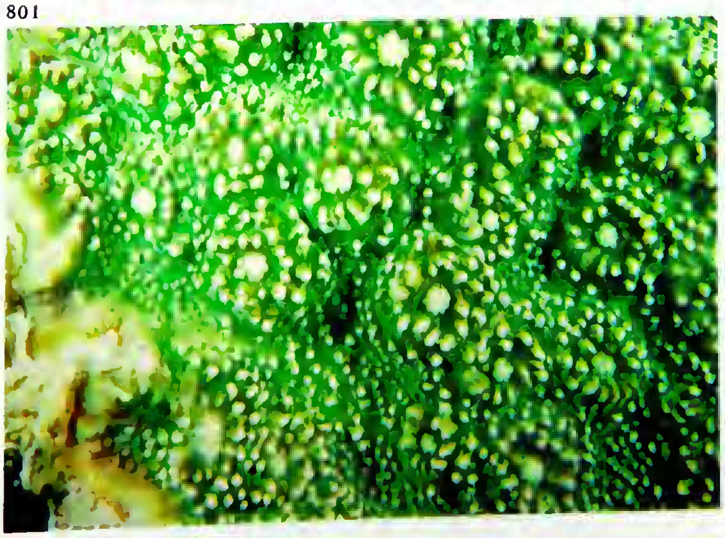

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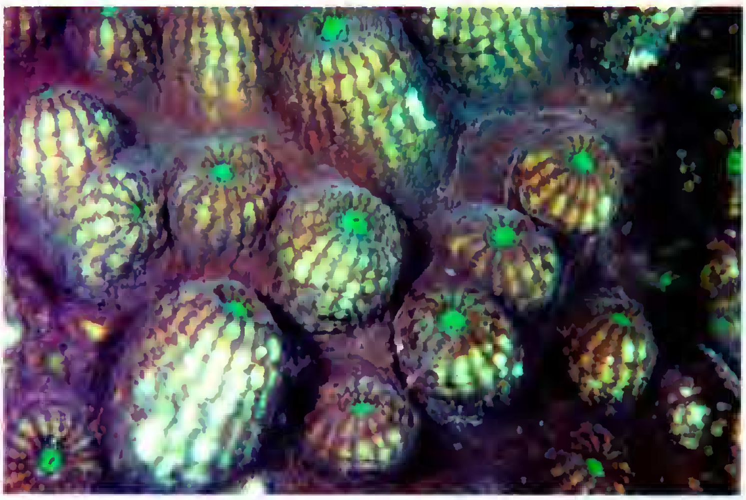

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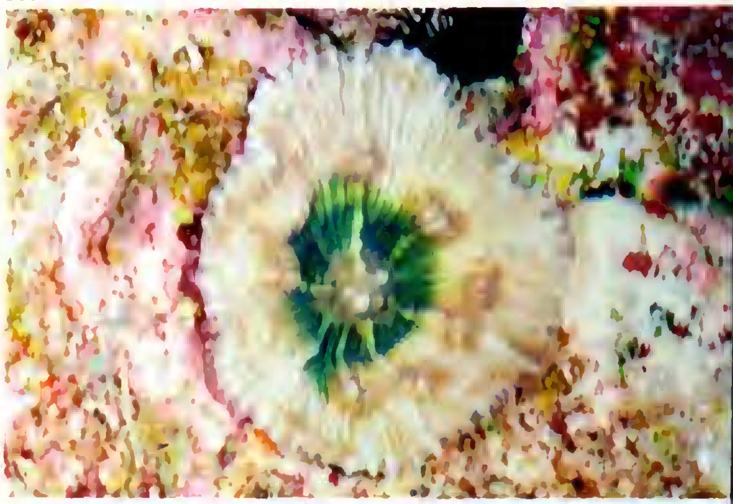

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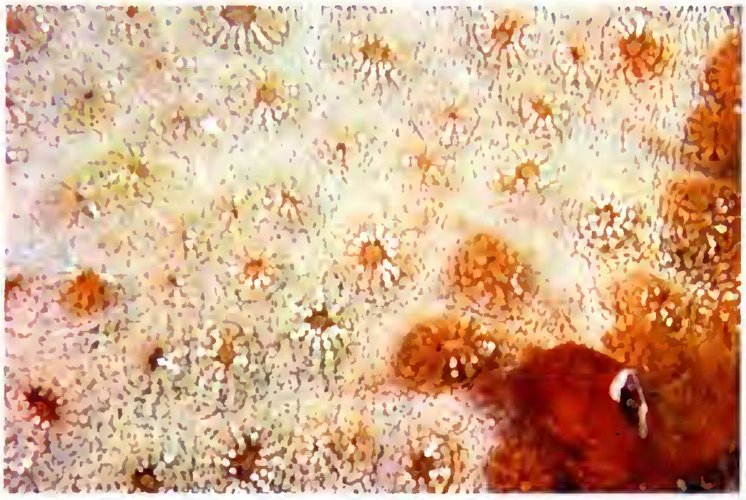

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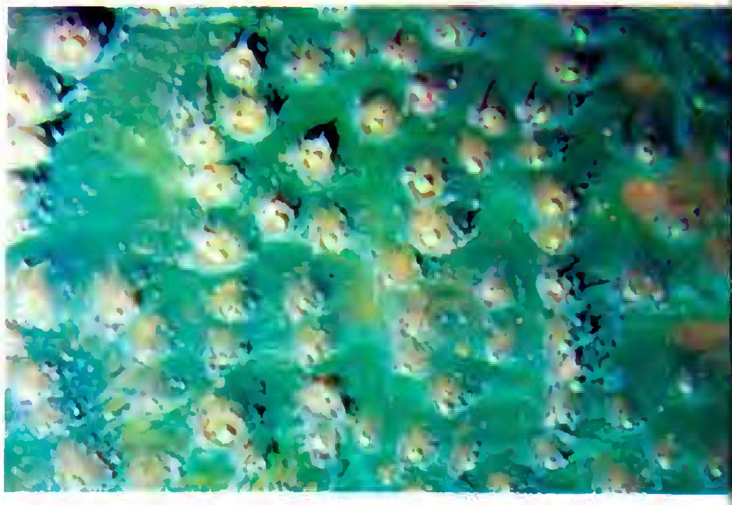

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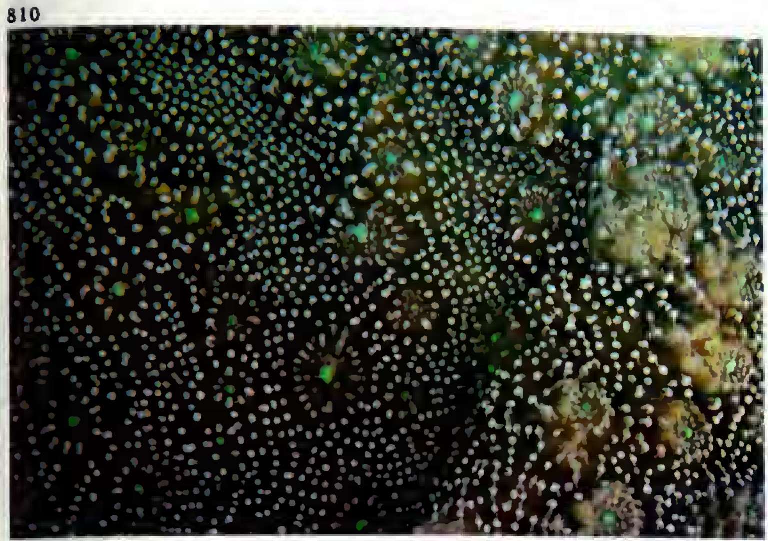

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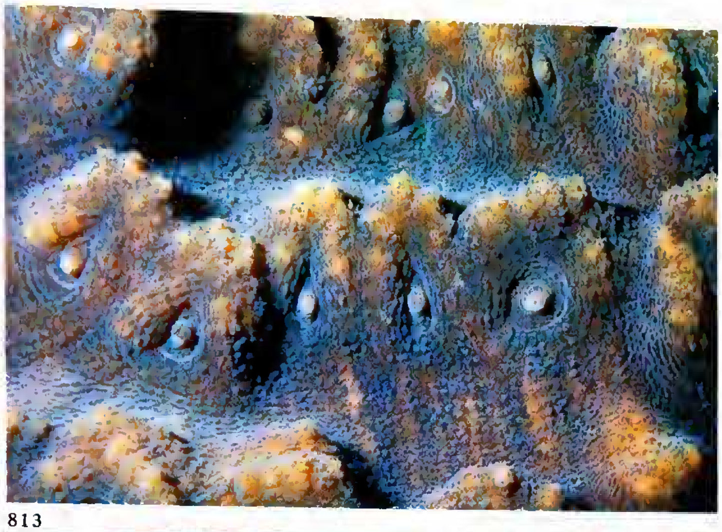

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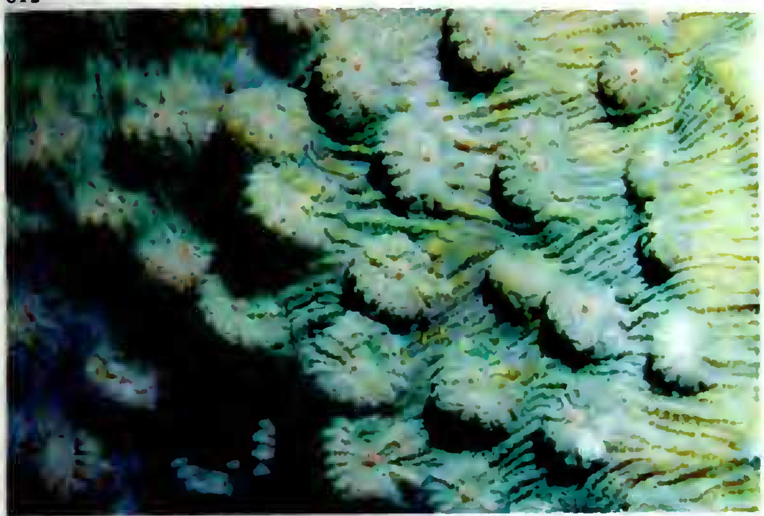

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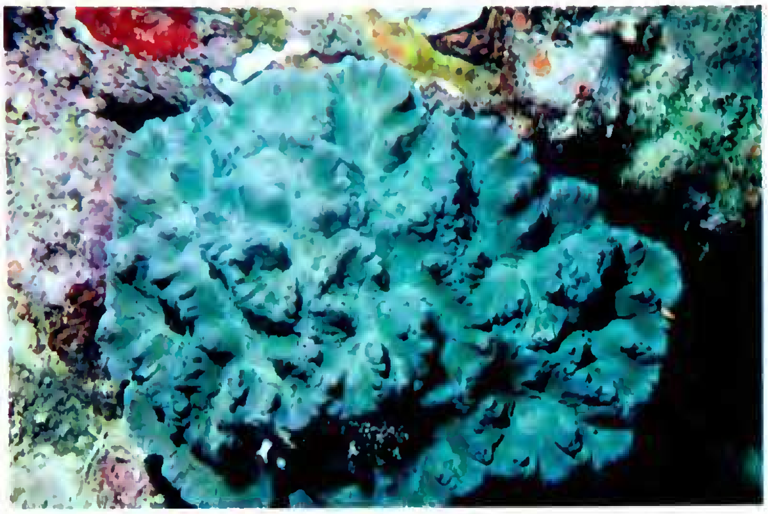

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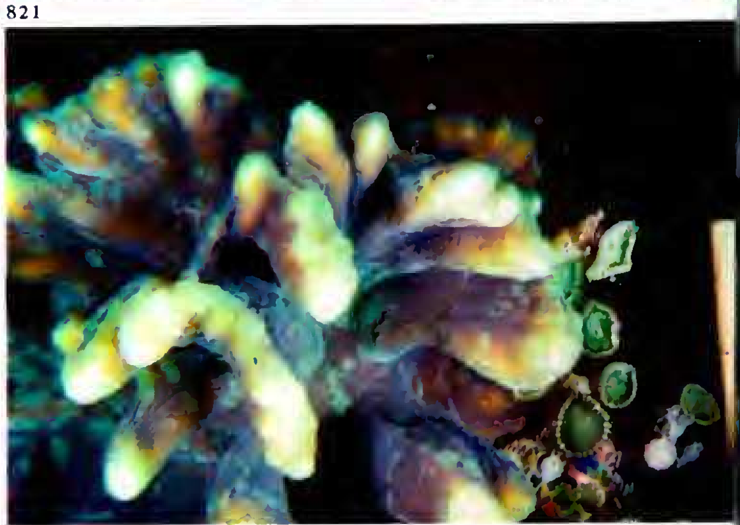

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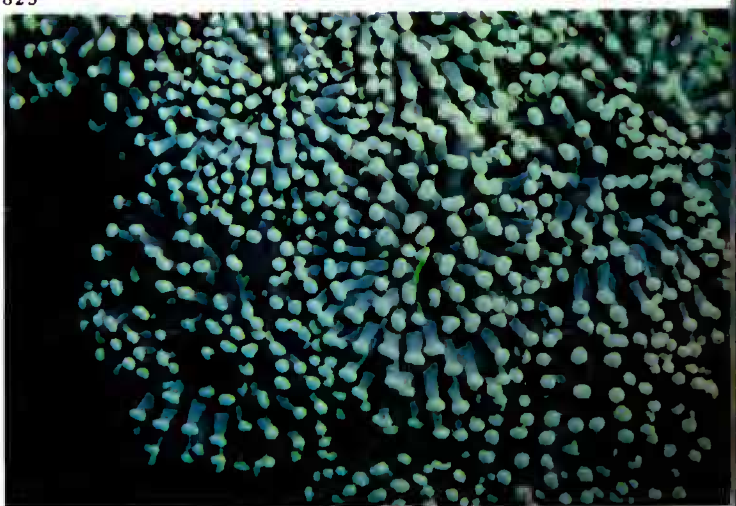

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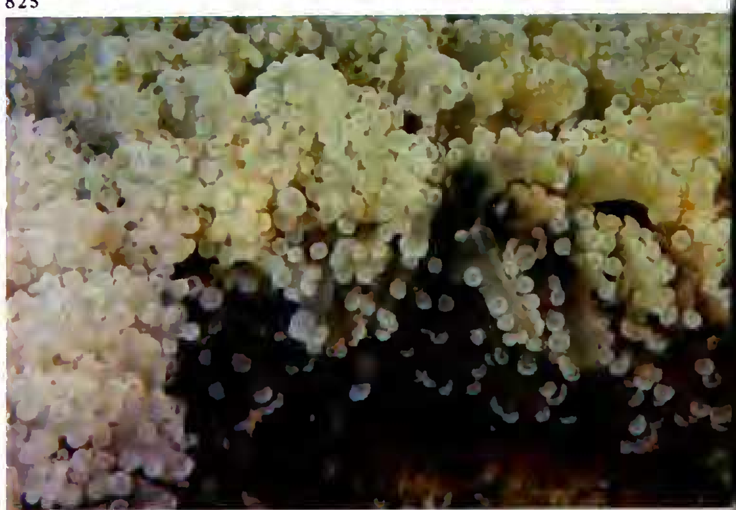

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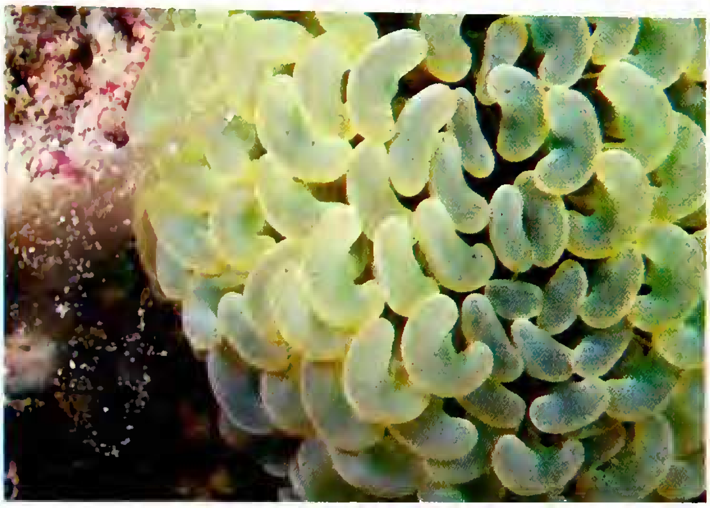
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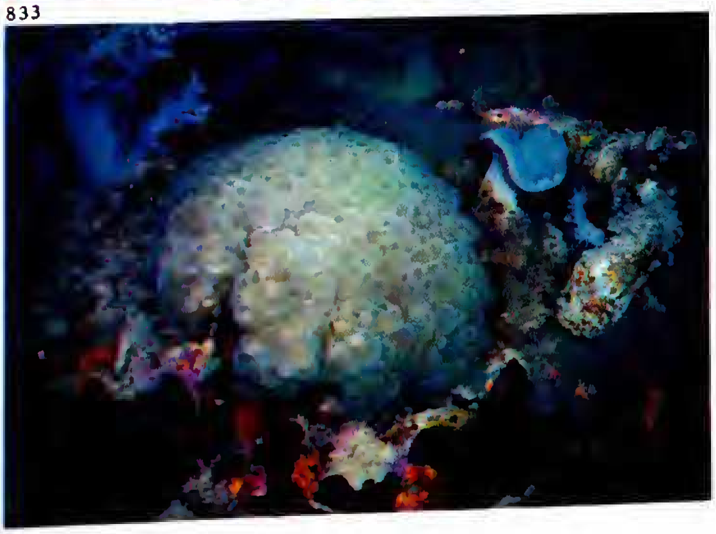

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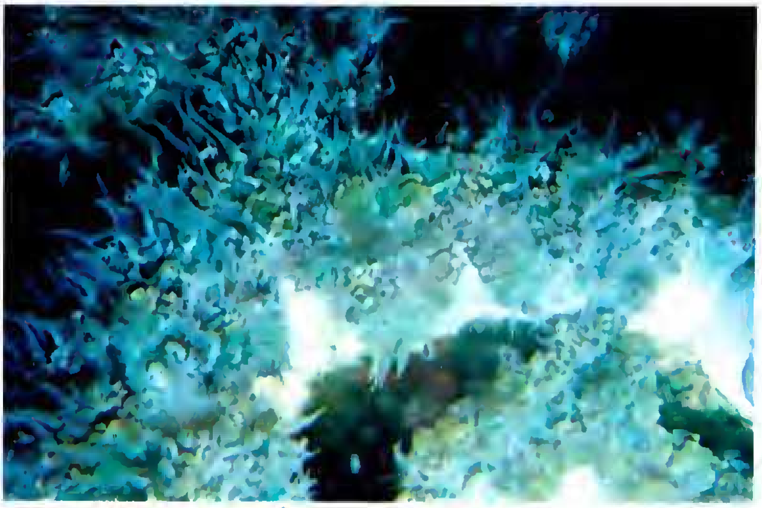

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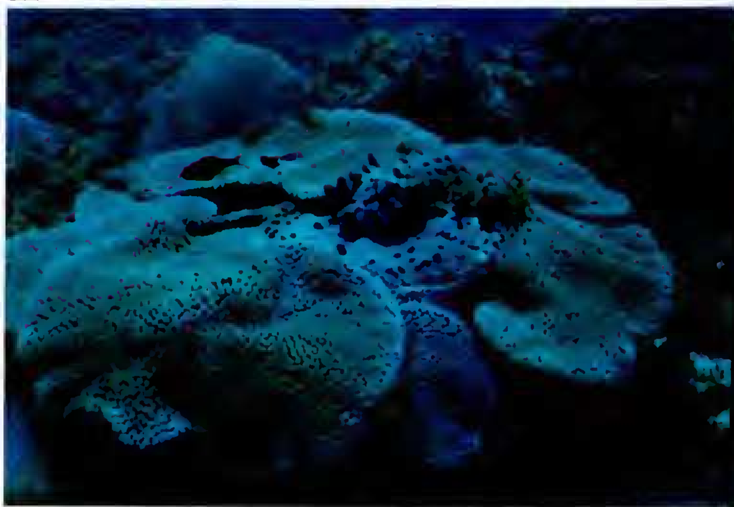

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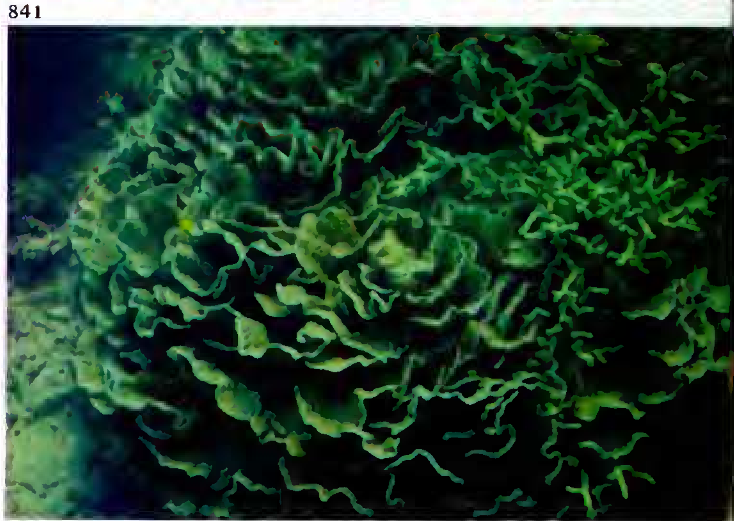

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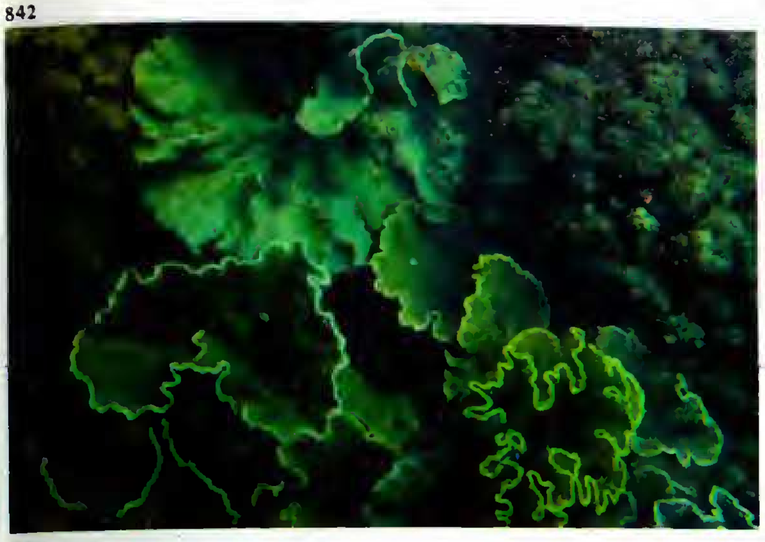

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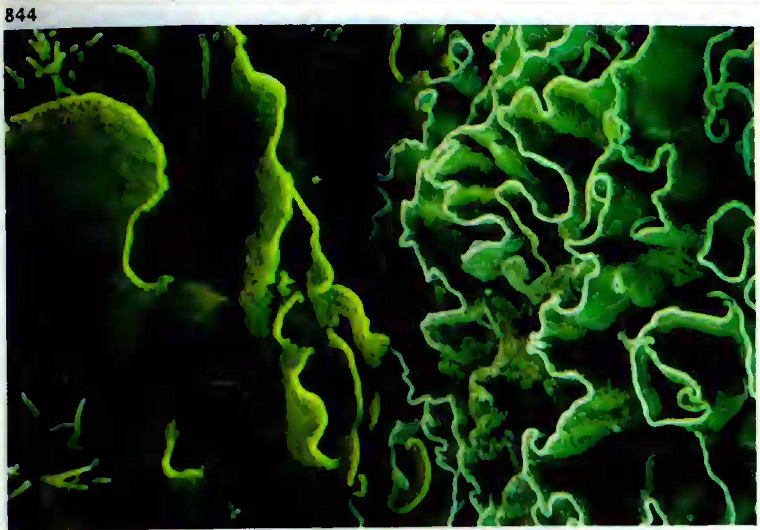

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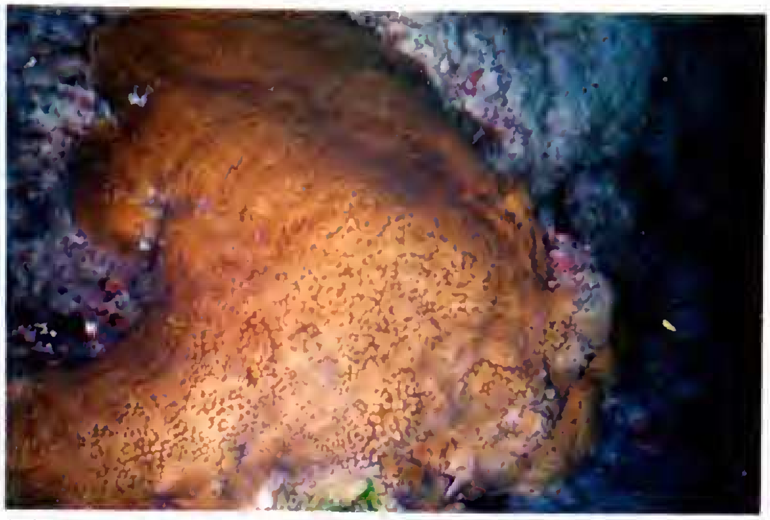

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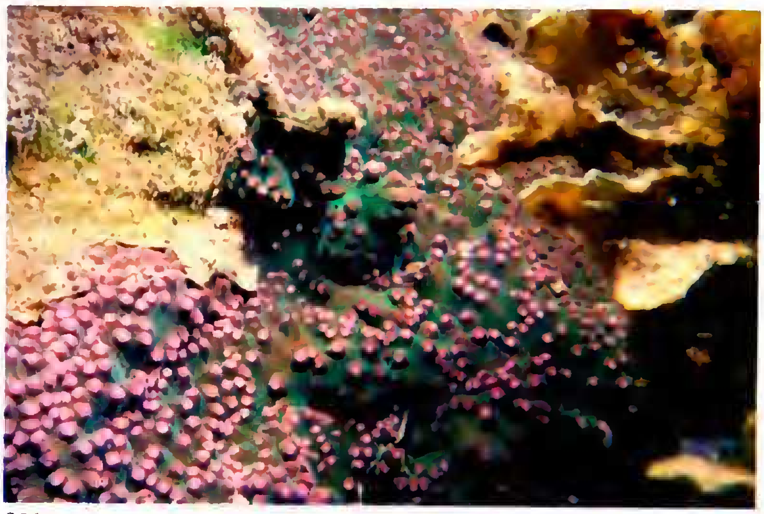

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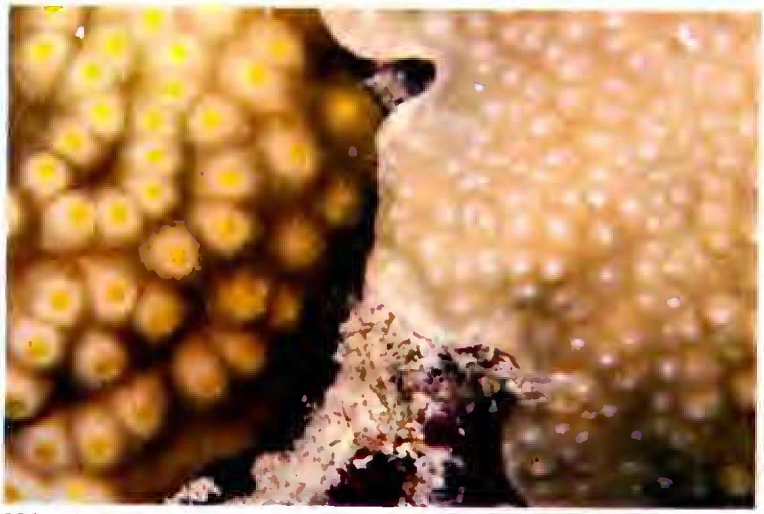

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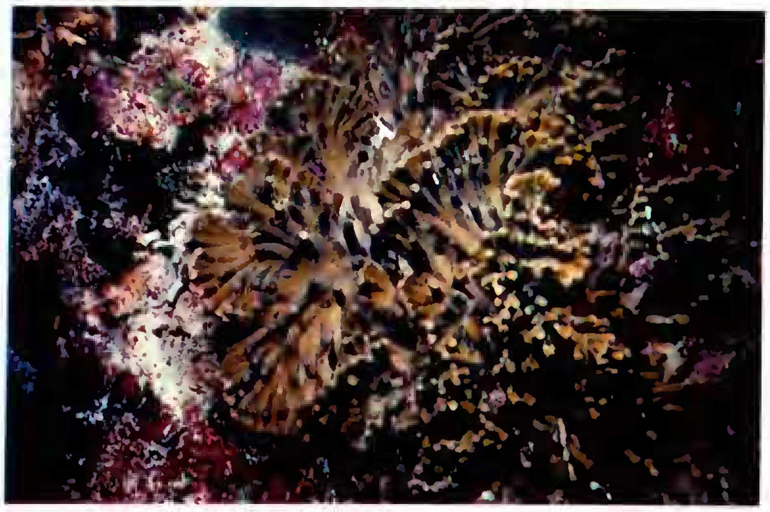

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Acknowledgments

The authors gratefully acknowledge the assistance of Mr Len Zell in all aspects of this study, including (unless otherwise indicated) all underwater photography. All laboratory photographic work was undertaken by Mr Les Brady, assisted by Mr Ed Lovell and Mr Zell. Preparation of the manuscript was greatly assisted by Mr Lovell, Ms Bette Willis, Ms Jean Weber, Ms Jennifer Amess and Ms Lindsay White.

The authors particularly acknowledge the hospitality and assistance offered by the British Museum (Natural History), the United States National Museum, the Museum National d'Histoire Naturelle, Paris, and also by Professor John Wells, Dr Paul Cornelius, Dr Brian Rosen, Dr Jean-Pierre Chevalier and Dr Maya Wijsman-Best.

Type species were studied in, or loaned by, the British Museum (Natural History); the United States National Museum; the Museum d'Histoire Naturelle, Paris; the Rijksmuseum van Natuurlijke Historie, Leiden; the University Museum of Zoology, Cambridge; the Museum of Comparative Zoology, Harvard University; the Department of Zoology, University of Glasgow; the Yale Peabody Museum, New Haven; the Australian Museum, Sydney; the Institute of Geology and Paleontology, Tohoku University; the Hessisches Landesmuseum, Darmstadt and Universitetets Zoologiske Museum, Copenhagen.

Specimens figured in the text were donated by Ms Zena Dinesen (Figs. 192, 193, 560), Dr Terry Done (Figs. 158, 336), Mr Alastair Birtles (Figs. 65, 66), all of James Cook University of North Queensland, Dr Walter Jaap, Marine Research Laboratory, Florida (Fig. 418), Mr Scoresby Shephard, South Australian Museum (Figs. 161, 425). Mr David Fisk, Heron Island Research Station (Figs. 184-187, 401, 402) and Dr Judy Land from a collection at the Discovery Bay Marine Laboratory (Fig. 419). Other material was gratefully received from Ms Carden Wallace (Queensland Museum), Dr Masashi Yamaguchi (University of Ryukyus), Professor Kei Mori (Tohoku University), Dr Stephen Cairns (United States National Museum), Sir Maurice Yonge (University of Glasgow), Dr van Soest (Rijksmuseum, Amsterdam) and Dr John Jell (University of Queensland).

This study was primarily supported by the Australian Institute of Marine Science. Support was also provided by the Australian Research Grants Committee and James Cook University Research Grants.

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